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UROMYCES IN A POPULATION OF *EUPHORBIA CYPARISSIAS*

By GILLIAN M. BUTLER

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The occurrence of *Uromyces scutellatus* (Schrank) Lév. on *Euphorbia cyparissias* L. and of *U. striatus* Schroet. on *E. cyparissias* and on various leguminous plants at a locality near Tuddenham, West Suffolk, is described.

On 9 May 1957 Dr D. E. Coombe collected specimens of *Euphorbia cyparissias* L. infected with a rust from a locality near Tuddenham, West Suffolk. This population of *E. cyparissias*, which is large and of long-standing, occurs in the short grassland of a training race-course and amongst the taller grass of the surrounding wooded verges. The middle of the race-course contains a field of lucerne and cocksfoot. The progress of rust infection in the population was followed through the summer.

FIELD OBSERVATIONS

Infected shoots of two distinct types were found with: (1) all infected leaves with abundant hypophyllous dark brown sori containing teleutospores; (2) all infected leaves with abundant hypophyllous spermagonia and a few to many hypophyllous or occasionally epiphyllous aecidia containing orange aecidiospores. The annual aerial host shoots arise as suckers from perennial underground stems and shoots. Both types of infected shoot showed similar morphological differences from healthy host shoots. Infected shoots were relatively tall and unbranched with occasional stem fasciations, bore more or less shorter, broader and yellower leaves, and did not flower. In general, shoots bearing spermagonia and aecidia were more deformed with yellower leaves than were shoots bearing teleutospores. Shoots with both types of infection together were not found and the two types were each distributed in separate patches throughout the population of *E. cyparissias*, forming 1–10 % of the population. Infection with spermagonia and aecidia was usually present on all shoots arising from adjacent suckers, whereas amongst clumps of shoots infected with the teleutospore stage some shoots were healthy and some were infected.

TELEUTOSPORE STAGE

The dark brown, round, blister-like sori were each surrounded after rupture by a torn white revolute margin of leaf tissue. Most sori contained, in addition to teleutospores with characteristic wall ornamentation of large, more or less longitudinally arranged warts, a small proportion of uredospores, each with fine spines and four germ pores, and also peridial cells.

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This rust agreed with the description by Tranzschel (1910) of *Uromyces scutellatus* (Schrank) Lév. Comparison with exsiccati in Kew Herbarium enumerated by Tranzschel confirmed this identification (Table 1). Spermagonia, which are stated by Tranzschel to be few to numerous or occasionally absent, were not found on shoots bearing teleutosori at Tuddenham.

Table 1. *Spore measurements (mean and range) of* Uromyces scutellatus *on* Euphorbia cyparissias

	Source of material			
	G. M. Butler, Tuddenham	Sydow, Ured. 8	Holl, Schm. et Kze., Deutsch. Schw. CXLV	Moug. et Nestler, Stirp. crypt. Vogeso-Ren. 93
	Teleutospores			
Length (μ)	25 (21–29)	24 (23–27)	27 (23–31)	24 (20–26)
Breadth (μ)	20 (18–22)	21 (19–22)	21 (18–25)	19 (16–21)
	Uredospores			
Length (μ)	23 (18–28)	24 (22–26)	—	—
Breadth (μ)	20 (16–24)	20 (18–23)	—	—

AECIDIOSPORE STAGE

Experimental evidence on the life cycle of *U. scutellatus* appears to be lacking and the occurrence of uredospores and of peridial cells with the teleutospores is used as evidence that the fungus is microcyclic (Tranzschel, 1910; Viennot-Bourgin, 1949). However, Tranzschel also provided observational evidence of an *-opsis* form of life cycle in *U. excavatus* (DC.) Lév., a species closely related to *U. scutellatus* but with aecidia and teleutosori on *E. verrucosa* Lam. In addition, the morphology of the spermagonia, aecidia and aecidiospores on the plants at Tuddenham agrees with the description of the aecidial stage of that group of closely related rusts of leguminous plants which are placed together by Hylander, Jørstad & Nannfeldt (1953) under the collective name *Uromyces pisi*, viz. *U. euphorbiae-corniculati* Jordi, *U. laburni* (DC.) Otth., *U. onobrychidis* Bub., *U. punctatus* Schroet., *U. striatus* Schroet. and *U. pisi* (DC.) Otth.

Accordingly, a search was made for rust infection of possible alternate hosts amongst the leguminous plants in the associated vegetation at Tuddenham. In June 1957 a few plants of *Medicago sativa* L., *M. lupulina* L. and *Trifolium campestre* Schreb. were found with scattered small brown sori on the upper and lower surfaces of the leaves and on the stems. Each of these plants was growing close to shoots of *E. cyparissias* bearing aecidia. Although infection of *M. sativa* and *T. campestre* remained slight, by 4 Oct. 1957 infection of *M. lupulina* was heavy with abundant sori on stems and leaves. Microscopical examination revealed the presence of uredospores and teleutospores on the *Medicago* spp. and of uredospores only on *T. campestre*. These agreed with the description of *U. striatus* Schroet. by Sydow (1910), and the identification was confirmed by comparison with exsiccati in Kew Herbarium (Table 2). Since Glasscock & Ware (1946) had reported that every British specimen of *U. striatus* on *Trifolium* spp. examined by them had proved to be *U. jaapianus* Kleb., the material on *T. campestre* was compared with *U. jaapianus* on *T. dubium* Sibth. in Cambridge University Herbarium. These differed in both size and morphology (Table 2) and the rust on *T. campestre* was ascribed more readily to *U. striatus*.

Table 2. *Spore measurements (mean and range) of* Uromyces striatus *and* U. jaapianus *on various leguminous plants*

	Material					
	U. striatus					*U. jaapianus*
	G. M. Butler, Tuddenham			Rabh., Fg. eur. 1479	Thuem., Myc. univ. 144	A. Smith
	T. campestre	*M. lupulina*	*M. sativa*	*M. lupulina*	*M. sativa*	*T. dubium*
			Teleutospores			
Length (μ)	—	20 (18–21)	19 (17–20)	22 (20–26)	20 (19–23)	—
Breadth (μ)	—	17 (15–19)	16 (16–17)	16 (15–18)	17 (16–19)	—
			Uredospores			
Length (μ)	20 (19–21)	20 (19–22)	21 (19–24)	22 (21–24)	—	24 (22–27)
Breadth (μ)	18 (17–20)	19 (18–20)	19 (17–20)	20 (18–21)	—	23 (21–24)
No. germ pores	3 (2–4)	3 (3–4)	4 (3–5)	3 (1–4)	—	6 (5–6)

At the same time a few test inoculations of leguminous plants growing at the Rockefeller Field Station of Cambridge Botany School were carried out using aecidiospores from *E. cyparissias* collected at Tuddenham. Inoculated plants were compared with nearby uninoculated plants in the field. Results of these inoculations are shown in Table 3. Although inoculations were not carried out under strictly controlled conditions, taken together with the field evidence there is little doubt that at least some of the aecidia on *E. cyparissias* and the infection of leguminous plants are stages in the life cycle of the same fungus, *U. striatus*.

Table 3. *Inoculation of leguminous plants with aecidiospores from* E. cyparissias

	Infection	Uredospores	Teleutospores
Inoculation A			
Medicago sativa	Slight	+	−
Inoculation B			
Medicago lupulina	Heavy	+	+
Pisum sativum	Slight	+	−

DISCUSSION

U. scutellatus has been recorded widely on *E. cyparissias* in continental Europe (Tranzschel, 1910), but the fungus has not been found in Scandinavia (Hylander, Jørstad & Nannfeldt, 1953). It is not recorded by Wilson & Bisby (1954) in their list of British Uredinales nor has any more recent reference to its occurrence in Britain been found. Grove (1913) excludes an obscure reference to *U. scutellatus* Lév. by Cooke (1878) as probably nothing but an error in identification. The presence of this rust at Tuddenham is the first record not only of *U. scutellatus* in Britain but also of any teleutospore stage of a rust fungus on *E. cyparissias* in Britain.

U. striatus is relatively widespread on *Medicago* spp. in Britain (Wilson & Bisby, 1954) as well as on the continent of Europe (Sydow, 1910) and in North America (Arthur, 1934), but the aecidial stage on *E. cyparissias* has not previously been reported from Britain. An aecidium of a rust on *E. cyparissias* was collected at Dover in 1909 (Grove, 1913). Although no evidence about the alternate host was available the specimen was ascribed to *U. pisi*. However, it may equally well belong to any one of the species within the *U. pisi* aggregate, including *U. striatus*.

The presence of this rust complex at Tuddenham is of interest in view of the evolutionary significance which has been attached to the occurrence on *Euphorbia* species of rust fungi with different life cycles but with morphologically similar teleutospores (Jackson, 1931). Moreover, the existence of variable life cycles has been demonstrated experimentally in several autoecious rust fungi (Wilson, 1948). Although experimental evidence is required to disentangle the life cycles, it is possible that the rust forms occurring at Tuddenham and assigned to *U. scutellatus* and *U. striatus* are not biologically isolated, a similar aecidial form providing opportunities for intermingling. It is noteworthy that although *M. lupulina* was the main alternate host for the heteroecious form, infection of several other leguminous plants took place.

Specimens have been deposited in Cambridge University (Nos. 75–77, 79, 80) and Kew Herbaria.

I wish to thank Dr N. F. Robertson for much helpful advice and Dr R. W. G. Dennis for help with material in Kew Herbarium.

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ON *ROBILLARDA PHRAGMITIS* SP.NOV.

By G. J. CUNNELL
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(With 3 Text-figures)

Robillarda phragmitis sp.nov. isolated from a submerged dead stem of *Phragmites communis* Trin. is described and illustrated with particular reference to the development of the spore and its appendage. Behaviour of single spore isolates on agar media and on sterilized pieces of *Phragmites* stems and *Carex* leaves is briefly noted.

Robillarda phragmitis sp.nov. (Figs. 1–3)

Pycnidia dispersa, immersa, ellipsoide, flavo-brunnea. Sporulae hyalinae, fusiformes, plerumque rectae, utrinque obtusae, magna 16–23 × 2·5–4 μ, medio 1-septatae, ad septa aut paulum aut non constrictae, 3 (4)-setae, filiformes, 15–23 μ longae.

Hab. In caulibus emortius submersis *Phragmitis communis*, circa Staines, Middlesex, in Anglia, July 1955. Typus Herb. I.M.I. 70678.

A few pycnidia of this fungus were found on a submerged piece of dead *Phragmites communis* stem collected from a gravel pit near Staines, Middlesex, in July 1955. Though most of the pycnidia were destroyed when sections and spore isolations were made the fungus grew readily on agar media and sterilized *Phragmites* stems and *Carex* leaves. The following description is based mainly on this cultured material.

The pycnidia found in nature on *Phragmites* stems are scattered, immersed and elliptical with the longest dimension parallel with the vascular strands. In vertical section (Fig. 1E) the wall is complete although somewhat irregular in outline. When the fungus is grown on sterilized *Phragmites* stems only a few pycnidia are formed in the surface mycelium, but on comparatively soft *Carex* leaves the numerous pycnidia (Fig. 1A, F) are immersed and occur singly or in groups. They are more or less elliptical and measure 150–320 × 100–200 μ (average of 50, 221 × 144 μ). The wall is 8–15 μ thick and mostly yellow-brown, although it is dark around the pore which measures 15–20 μ across. The outer layers are composed of flattened cells with thin, light-brown walls (Fig. 1D). In surface view these cells are angular, isodiametric, 4–8 μ across (Fig. 1C). The abundant pycnidia formed by cultures on oatmeal agar (Fig. 1B) are much larger than those found in nature or produced on *Carex* leaves and measure 240–530 × 200–470 μ (average of 50, 383 × 318 μ). They occur embedded in the agar either singly or in conspicuous clusters.

The spores are closely packed and embedded in mucilage within the pycnidial cavity, but are easily separated when the mass is mounted in water. The mature spores (Fig. 2A) are fusiform, straight or rarely slightly curved, and have thin, smooth, colourless walls which are not, or slightly

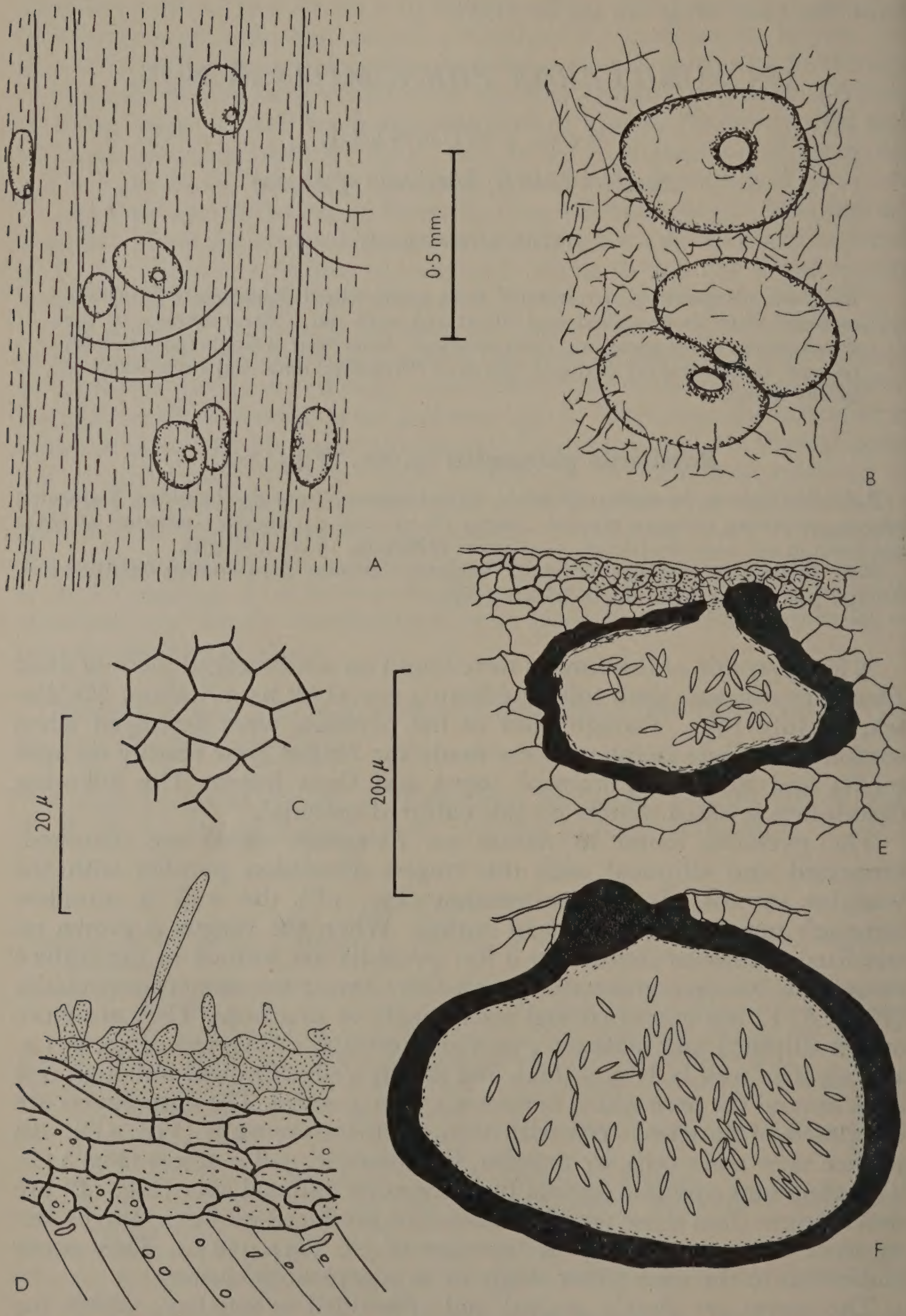

Fig. 1. *Robillarda phragmitis.* A, pycnidia formed on re-infected *Carex* leaf (× 50); B, pycnidia formed on 2% malt agar (× 50); C, surface view of pycnidial wall (× 1300); D, vertical section of pycnidial wall (× 1300); E, vertical section of pycnidium on *Phragmites* stem from nature (× 300); F, vertical section of pycnidium formed on re-infected *Carex* leaf (× 300).

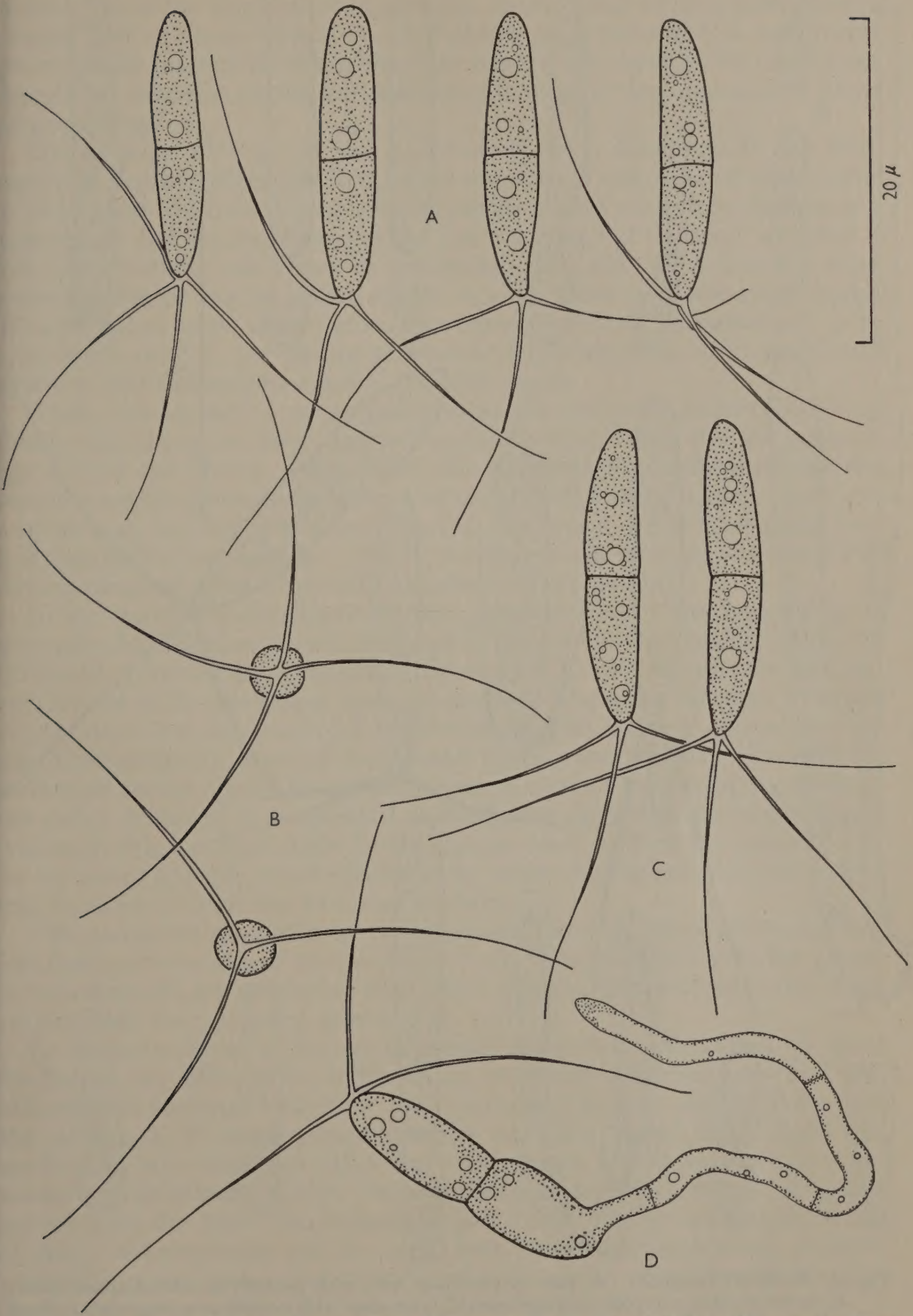

Fig. 2. *Robillarda phragmitis.* A, four living spores from nature; B, end view of two spores from nature showing positions of the setae; C, two living spores from pycnidia formed by culture on 2% malt agar; D, germinating spore after 18 hr in water at room temperature. (All × 2175.)

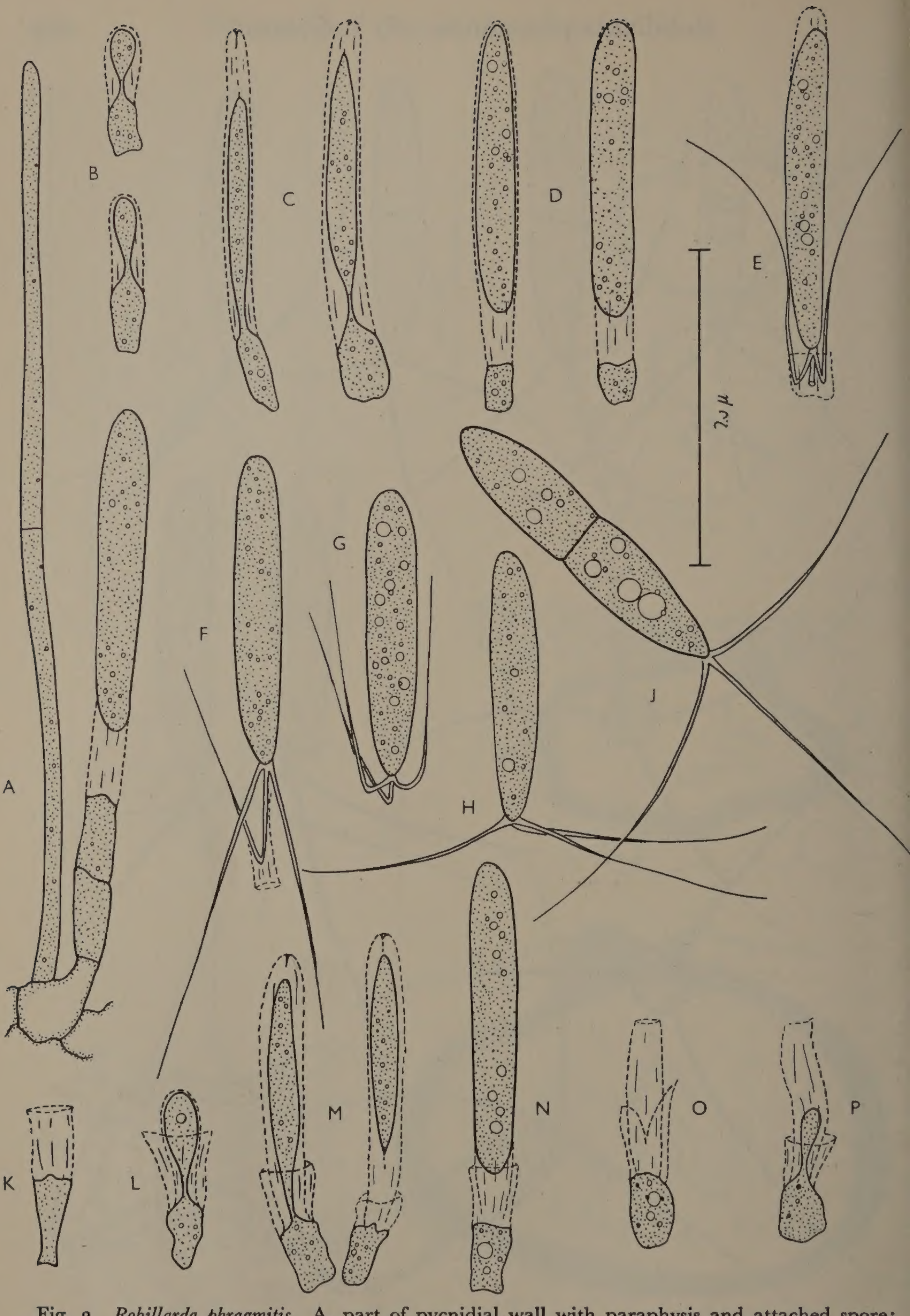

Fig. 3. *Robillarda phragmitis.* A, part of pycnidial wall with paraphysis and attached spore; B, very early stage in spore development; C, later stage with cytoplasmic connexion to basal cell constricted; D, older attached spores with cytoplasmic connexion to basal cell broken; E, detached spore with appendage apparent and basal and distal 'caps' still present; F–H, immature spores with appendages in various positions; J, mature septate spore; K, basal cell after detachment of spore; L–N, stages in development of second spores from the basal cells; O, basal cell after detachment of second spore; P, early stage in development of a third spore. (All × 2175.)

constricted at the single median septum. A few small oil drops are usually present and the somewhat dense cytoplasm gives the spores a pale olive-green colour, especially when they are seen in the mass. One end of the spore is rounded or obtuse and the other is more or less obtuse and bears an appendage.

This consists of 2–4, usually 3, setae, 15–23 μ long, which are thin, tapering, flexible, divergent and joined together at the point of attachment to the spore. In most water mounts pressure of the coverslip flattens the appendage and the setae are pushed into the plane of the spore axis but if this is prevented, end views of the spores (Fig. 2B) show that the setae project more or less at equal angles to each other and the spore body. Thus a spore with three setae approximates to the tetraradiate form commonly seen in the spores of aquatic hyphomycetes such as *Heliscus aquaticus* and *Clavariopsis aquatica* (Ingold, 1942).

When viewed with a horizontal microscope the spore always sinks very slowly with the spore itself directed vertically downwards and the appendage spread out above. Presumably the appendage greatly increases the resistance of the spore to the water and prevents it sinking rapidly. Further, a spore may be held at the water surface by means of the appendage and it is then difficult to dislodge. Hence the appendage may act as a floatation device assisting spore dispersal in surface water currents.

In the published literature on the genus *Robillarda* the appendage is generally described as apical, although it is not clear whether it is borne on the basal or distal end of the spore. Sprague & Cooke (1939) state that the appendage of *R. agrostidis* is borne at the tip of the spore but later Sprague (1951) describes the spore of *R. muhlenbergiae* with a basal appendage and says that probably those of the former species are similar. He bases his statement on the orientation of the spores in crushed pycnidia, but to settle the point definitely it is essential to study the development of the spore. Although this has been done for the fungus dealt with in this paper, it will be necessary to study other species in the same way before any conclusions can be drawn about the genus as a whole.

The spores are produced by the innermost layer of thin-walled, more or less isodiametric cells of the pycnidial wall. Intermingled with the young attached spores are numerous long, thin, septate, unbranched hairs which project into the pycnidial cavity (Fig. 3A).

In water mounts of living, unstained material early stages of spore formation are difficult to see with an ordinary compound microscope, although in aqueous methylene blue young spores take up the stain and the sequence of development can be partially made out. However, methylene blue does not stain the appendages and it causes a certain amount of shrinkage. Other stains used (gentian violet, lignin pink, fast green) have the same disadvantages, and finally it was found that details of spore development can be seen best by examining young crushed pycnidia, mounted in water or 10 % gelatine, with a phase-contrast microscope and using a blue light source (Ilford filter micro 2, 303).

The young spore first appears as a rounded projection from the centre of the wall cell and, with increase in size, its cytoplasmic connection with the basal cell becomes very attenuated (Fig. 3B). At this early stage the spore possesses a transparent outer wall which is thin distally but thick at the narrow connexion between the spore and its basal cell. The spore then elongates but at first there is little increase in width. At the distal end the outer wall becomes thick and extends some distance beyond the cytoplasm of the spore. A small refractive spot can often be seen at the tip of the outer wall and it is sometimes possible to see a thin line extending from this to the body of the spore (Fig. 3C). With further enlargement the outer wall becomes stretched and it becomes difficult to see at the sides and distal end of the spore. The cytoplasmic connexion with the basal cell is then completely severed although the spore remains firmly attached by the thick outer wall at its proximal end (Fig. 3D). At this stage the spore is aseptate and more or less cylindrical and becomes detached due to the transverse division of the transparent region connecting it to the basal cell.

It is only after detachment of the spore that the appendage can be seen. Presumably this is formed from strips of the outer wall which curve away from the sides of the spore at, or soon after, detachment, leaving an apical cap which soon disappears (Fig. 3E). The proximal parts of the appendage are apparently organized within the basal transparent region where they are bent back to join each other and the end of the spore. The transparent proximal cap is pushed off as the arms of the appendage straighten out (Fig. 3F). Occasionally spores are seen with the setae still bent back after the terminal caps have disappeared (Fig. 3G). Further development of the spore to maturity involves increase in size, the appearance of conspicuous oil drops and the formation of a single, distinct septum (Fig. 3H, J).

Many basal cells have been seen with the remains of the proximal portion of the outer transparent wall still attached after detachment of the spore (Fig. 3K). Apparently the basal cell may produce a second or even a third spore. These later spores develop in essentially the same way as described above but the remains of the outer wall of the first spore forms a collar at the base (Fig. 3L–P).

The spores germinate slowly at room temperature in water or on 2 % malt agar. The cells swell and the spores appear to be very constricted at the septa. At first a single germ tube is produced, usually from the distal end of the spore (Fig. 2D).

On 2 % malt agar a slow-growing colony with an irregular edge is formed. The whitish aerial mycelium is thin and even but almost absent from the marginal region. The central, older part of the colony is pale orange. On oatmeal agar the colony is similar but on potato-dextrose agar the growth rate is much lower and a pale colony almost devoid of aerial mycelium is formed. Fruiting is abundant on 2 % malt agar and oatmeal agar but poor on potato-dextrose agar. When grown in the light on 2 % malt agar there is a pronounced zonation of pycnidia, with a dense ring followed by one with very few fruit-bodies, but in the dark the pycnidia are fairly evenly distributed. No marked zonation of pycnidia is found in colonies on oatmeal agar when grown in the light or in the dark. Sectoring occurs on all three media with the production of faster growing, sterile zones with little aerial mycelium.

Dimensions of 100 spores, excluding the appendages, taken at random from three sources are:

	Length (μ)			Width (μ)	
Source	Range	Mean	Standard deviation	Range	Mean
Phragmites communis from nature	16·0–23·0	18·5	1·23	2·5–4·0	3·4
2% malt agar	15·0–21·0	18·1	1·51	3·0–4·5	3·8
Re-infected *Carex*	14·0–24·0	17·2	1·49	3·0–4·5	3·5

As far as can be ascertained this is the first time that a *Robillarda* sp. has been recorded in the British Isles or on *Phragmites communis*. Since Saccardo (1882) first described the genus based on *R. sessilis* Sacc. (= *Pestalozzia sessilis* Sacc.) only some fourteen species have been described from various parts of the world and on various substrata. Most of the earlier described species have spores much smaller than those of my material. Although *R. celtidis* Scalia (spores 17–21 × 4–5 μ, 2–3 setae, on dead stems of *Celtis australis*, Sicily) (Saccardo, 1906) and *R. geasteris* Hollós (spores 18–20 × 3–3·5 μ, 2–5 setae, on exoperidium of *Geaster* spp., Hungary) (Saccardo, 1913) have spores which are similar in size to those which I have found, the very different substrata on which they occurred suggests that they are different species.

Three species have been recorded on members of the Gramineae but *R. graminis* Höhn. (on sheaths of *Festuca ovina* Germany) (Saccardo, 1906) has 8–12 divergent setae and *R. muhlenbergiae* Sprague (spores 12–16 × 3·4–3·8 μ, 3 setae, on dead sheaths of *Muhlenbergia filiformis*, North America) (Sprague, 1951) has shorter spores. The spores of my fungus are very similar to those of *R. agrostidis* Sprague (spores 17·5–20 × 2·6–3·3 μ, 3–4 setae, on dead leaves and sheaths of *Agrostis tenuis*, North America) (Sprague & Cooke, 1939) but as Sprague (*in litt.*) has pointed out, they are thicker, having the width of *R. muhlenbergiae* spores and exceeding those of *R. agrostidis* in length. Further, the pycnidia of *R. agrostidis* are black-brown, obscurely ostiolate and with a thin brittle wall of deeply pigmented, black-brown cells whereas in my material the pycnidia are pale yellow-brown, clearly ostiolate and have thin soft walls of yellowish-brown cells. Thus, although this fungus is very similar to *R. agrostidis* it appears to be sufficiently distinct to warrant describing it as a new species.

Dried cultures on agar have been deposited at the Commonwealth Mycological Institute, Kew and at the Herbarium, Royal Botanic Gardens, Kew. Living cultures have also been sent to the Commonwealth Mycological Institute and the Centralbureau voor Schimmelcultures, Baarn, Netherlands.

I wish to express my gratitude to Prof. C. T. Ingold for his interest and encouragement in this study. My thanks are also due to Dr R. Sprague of the Tree Fruit Experiment Station, Wenatchee, Washington, U.S.A., who examined my material and gave helpful advice.

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FLUMINISPORA OVALIS INGOLD ANTEDATED BY *DIMORPHOSPORA FOLIICOLA* TUBAKI

Fluminispora ovalis was described in the September number of the current volume of these *Transactions* (see pp. 369–71). In July Tubaki (*J. Hattori Bot. Lab.* **20**, 156, 1958) described what is clearly the same fungus under the name *Dimorphospora foliicola*. His excellent account and figures leave no doubt that we both were concerned with the same aquatic hyphomycete.

C. T. INGOLD

Trans. Brit. mycol. Soc. **41** (4), 413–418 (1958).

A CONSIDERATION OF THE SPECIES OF *PHOMA* WHICH PARASITIZE POTATOES

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(With Plate 22)

Information from the literature and data obtained from a study of *Phoma* isolates from potatoes is presented as evidence that *P. solanicola* Prill. & Delacr., *P. tuberosa* Melhus, Rosenbaum & Schultz and *P. foveata* Foister should be regarded as one species, *P. solanicola*. *P. eupyrena* Sacc. is regarded as a separate species.

Four of the *Phoma* species described from the potato, *P. eupyrena* Sacc., *P. solanicola* Prill. & Delacr., *P. tuberosa* Melhus, Rosenbaum & Schultz and *P. foveata* Foister, have been recorded as parasites. *P. eupyrena* was described from stems (Saccardo, 1879), but it has never been shown to be parasitic on the aerial parts of the plant. This fungus has been reported as a parasite on tubers (Wollenweber, 1920), but its pathogenicity to this organ has not been confirmed (Shapovalov, 1923; Dennis, 1946). *P. solanicola* was originally credited with causing a disease of potato stems in France (Prillieux & Delacroix, 1890) and has been recorded on potato stems in Germany (Köhler, 1928), Britain (Dennis, 1946; Moore, 1947) and Denmark (Hellmers, 1952). Attempts to prove its pathogenicity to stems have failed (Köhler, 1928; Hellmers, 1952), but Dennis (1946) has shown the species to be pathogenic to tubers. *P. tuberosa* was described as the cause of a dry rot of potato tubers in North America (Melhus, Rosenbaum & Schultz, 1916), and has subsequently been reported on tubers in Europe where its pathogenicity has been confirmed (Van Poeteren, 1928; Dennis, 1946; Moore, 1947). Foister (1940) described *P. foveata* as the organism causing gangrene, a tuber rot of the potato first recorded in Scotland (Alcock & Foister, 1936). This species was stated to differ from *P. eupyrena*, *P. solanicola* and *Phomopsis tuberivora* Güss. & Foster in culture but no comparison with *P. tuberosa* has been recorded.

In an examination of *Phoma* isolates obtained from potatoes, considerable variation was observed in their general appearance in culture. *P. eupyrena*, as recognized by Wollenweber, could be identified by its formation of abundant and characteristic chlamydospores, but attempts to assign isolates to *P. solanicola*, *P. tuberosa* and *P. foveata* met with difficulty. Therefore, a reinvestigation of the *Phoma* parasites of the potato was considered desirable.

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DIFFERENTIAL CRITERIA USED IN THE SEPARATION OF *PHOMA* SPECIES

The methods used in assigning isolates of *Phoma* to their species are generally considered to be unsatisfactory. The classification adopted is that of Saccardo (1884) in which the determination of the species is based on the host species and organ involved. Thus, on the potato, *P. solanicola* which was described from stems, is separated from the tuber parasites *P. tuberosa* and *P. foveata*. Such a system is not applicable to species which occur on the same organ; therefore, additional criteria, such as the macroscopic appearance of the fungus in culture, and the shape, size and colour in the mass of the spores, have been taken into account in their identification.

DESCRIPTIONS OF *PHOMA* SPECIES PARASITIZING POTATOES

No type culture of *P. solanicola* Prill. & Delacr. is available and the description of the fungus is inadequate for use in its identification. The species may, however, be recognized from the description given by Köhler (1928) of material from haulms. When *P. tuberosa* was erected, no authentic specimens of the previously described *Phoma* parasites of the potato were available for comparison. The species was based on the difference between the size of its spores and those of the existing *Phoma* species on potatoes. It was suggested by Grove (1935) that *P. solanicola* and *P. tuberosa* may be the same organism and Dennis (1946), in grouping his isolates from various hosts, regarded *P. solanicola* and *P. tuberosa* as identical. Moore (1947), sharing this view, suggested that the earlier and correct name of the fungus is *P. solanicola* Prill. & Delacr. sensu Köhler.

P. foveata has generally been accepted as a distinct species, characterized by the formation of its pycnidia on pseudo-subicular sheets. However, in the text accompanying the description of *P. tuberosa*, the pycnidia of the fungus were recorded as being formed on mycelial mats (Melhus *et al.* 1916); therefore, the possession of a pseudo-subiculum cannot be accepted as diagnostic of *P. foveata*.

P. eupyrena was described from potato stems, but subsequent work with this species has been with isolates from potato tubers (Wollenweber, 1920; Shapovalov, 1923; Dennis, 1946). Chlamydospores were not recorded in Saccardo's description of *P. eupyrena*, but the species, as interpreted by Wollenweber (1920), has been identified by the characteristic chlamydospores which are formed in pairs or short chains throughout its mycelium.

The salient features of the spores of the *Phoma* parasites of the potato have been taken into consideration by various authors in determining the species. The data presented for a species by any one author have generally been in agreement with those given by others for the same species. In addition, an examination of the information available for any one of the species, excluding *P. eupyrena*, usually shows it to be in agreement with the characteristics given for the other two species.

Differences in the size of the spores have frequently been used in differentiating among the species, e.g. in the separation of *P. tuberosa* and *P. solanicola* (Melhus *et al.* 1916). The differences in measurement of extruded and unextruded spores, given by Köhler (1928) for the former species, indicates the importance of taking maturity into account. Moreover, the rate of spore maturation is known to vary both between species and among different isolates of the same fungus, e.g. strain 1, regarded by Dennis (1946) as *P. foveata*, and the original isolate of *P. foveata*. Therefore, too much emphasis cannot be placed on minor differences in spore measurement in defining the species.

OBSERVATIONS ON NAMED SPECIES OF *PHOMA*

To aid identification of the isolates from potatoes and to facilitate a comparison of the species, cultures of *P. solanicola*, *P. tuberosa* and *P. foveata* were obtained from the Centraalbureau voor Schimmelcultures, the American Type Culture Collection, and Dr C. E. Foister, respectively.

Phoma solanicola

The culture of *P. solanicola* received from Baarn was no longer in a sporing condition and it was never observed to form pycnidia. This may have been a mycelial strain which had arisen by the 'dual phenomenon' (Hansen, 1938), shown by Dennis (1946) to be evident in the species. On potato-dextrose agar and malt agar, growth was regular and the fungus formed a white mycelial mat which rapidly darkened to give a black to olive basal plectenchyme with a short greyish to white aerial mycelium. The darkening of the cultures was due to pigmentation of the walls of old thickened hyphae. There was no production of a diffusible pigment in the culture medium. The fungus was not pathogenic to potato stems and tubers.

Phoma tuberosa

The mycelial characteristics of *P. tuberosa* were similar to those of *P. solanicola* but, in addition to the pigment deposited on the hyphal walls, the fungus produced a diffusible brown pigment in the culture medium. In the course of culturing, colonies which did not produce pigment in the medium separated out, and these cultures were identical with the culture of *P. solanicola* from Baarn. Mature pycnidia were never produced on agar slants but knots of thick, dark hyphae, which may have been immature pycnidia, were invariably present. This fungus produced typical gangrene lesions on inoculated potato tubers and caused extensive lesions on potato stems. Mature subepidermal, subglobose, ostiolate pycnidia formed on potato stems and extruded tendrils of ovoid, biguttulate pycnospores measuring 6·4 × 2·4 (5·8–7·0 × 2·0–2·9) μ.

Phoma foveata

On potato-dextrose agar and malt agar, *P. foveata* produced a dense, white, aerial mycelium which soon darkened, beginning at the centre of the colony. The individual hyphae became olive brown to black, due to a surface deposit of pigment, but the entire plectenchyme appeared teak coloured, due in part to the production of a brown diffusible pigment in the culture medium. The aerial mycelium was grey to buff with a tendency to darken. Pycnidia were not produced on artificial culture media. The fungus was pathogenic towards potato tubers, and extensive lesions with ripe, subepidermal, subglobose, ostiolate pycnidia developed on inoculated stems. The ovoid, biguttulate pycnospores from potato stems measured 6·2 × 2·6 (5·8–6·5 × 2·1–2·8) μ.

OBSERVATIONS ON ISOLATES OF *PHOMA* FROM POTATOES

Some 400 isolates of *Phoma* were obtained from potato tuber rots and from green, senescent and dead potato stems in Britain and the United States. Among the isolates which did not cause rotting when inoculated into potato tubers, *P. eupyrena*, as recognized by Wollenweber, could be identified by the characteristic chains of black chlamydospores formed throughout the mycelium. Although chlamydospores were not recorded in the description of *P. eupyrena* (Saccardo, 1879) they have been accepted as characteristic of the species in subsequent work (Wollenweber, 1920; Shapovalov, 1923; Dennis, 1946). In an examination of *P. eupyrena* on *Solanum dulcamara* from the Saccardo Herbarium, chlamydospores were not observed. Therefore, the identification of the organism bearing chlamydospores as *P. eupyrena* would seem open to question.

The isolates which were pathogenic when inoculated into potato tubers were of two types, irrespective of the substrate from which they were isolated. One type like the *P. foveata* described above, was characterized by the production of a brown diffusible pigment in the culture medium (potato-dextrose agar or malt agar), while the other, which was similar to the *P. solanicola* from Baarn, was morphologically identical with it but did not pigment the medium. The mycelial characteristics were similar to those of *P. solanicola*, *P. tuberosa* and *P. foveata* described above.

The degree of pigmentation in those isolates which produced the diffusible pigment was observed to vary from one isolate to another, and occasionally among transfers from one culture. Among the British isolates, in cultures where the colouring was most intense, greenish yellow crystals formed in the culture medium, particularly in the region of old hyphae, and sometimes they were so abundant that they dominated the colour of the colony. The formation of pigment and crystals also varied with the nutritional state of the fungus. In Dox agar without any carbohydrate present, the hyphae were normal but pigment and crystals were not produced. With the addition of 1 % glucose, sucrose or maltose to the medium, pigmentation occurred. When 3 % or 5 % of these carbohydrates were present, pigmentation was more intense, the hyphae became encrusted with greenish yellow crystals, growth was irregular and large, multicellular chlamydospores formed.

Further observations on pigmentation were made with monospore isolations from a single pycnidium of a strongly pigmented isolate. In the resulting colonies, thirteen did not produce any pigment, and in the remaining seventy-four pigment was produced with varying degrees of intensity. The appearance of the colonies was maintained through several series of transfers.

Sporulation in the isolates was variable and generally sparse. The pycnidia which formed in artificial media arose from knots of large, thick hyphae, partially submerged in the medium. They were thin, parenchymatous, brown to black and varied in shape. Multilocular pycnidia with several ostioles were occasionally observed. In the mass the spores varied from flesh coloured to salmon pink and the colour appeared most intense in strongly pigmented cultures. Individually the spores were hyaline, ovoid and mostly biguttulate; however, the guttules were not always apparent under the low power of the microscope and occasionally only one or more were present in spores taken from the same pycnidium. Spores from pigmented cultures measured 6·2 × 2·5 (5·6–7·3 × 1·7–4·7) μ, and those from unpigmented cultures measured 6·5 × 3·0 (5·3–7·7 × 2·3–3·7) μ.

On potato tubers pycnidia were formed beneath the epidermis and embedded within the the rotted tissue. The subepidermal pycnidia were formed singly or in groups and frequently on a mass of undifferentiated mycelium. They were thick walled, globose, brown to black in colour, and erumpent when mature. Among the American specimens, considered to represent *P. tuberosa*, the pycnidia were frequently formed on a subiculum (Pl. 22). Similar tissue was illustrated by Dennis (1946) for the strain which he regarded as this species; therefore, the presence of a pseudo-subiculum cannot be accepted as diagnostic of *P. foveata*. On potato stems the pycnidia were thin walled, erumpent and formed singly or in groups. Each was provided with a distinct ostiole (Pl. 22).

DISCUSSION

It has been shown that some authors have regarded *P. solanicola* and *P. tuberosa* as one species but so far *P. foveata* and *P. eupyrena* have been considered distinct.

In the present investigation *P. eupyrena*, as interpreted by Wollenweber, was considered to be a distinct species. However, the identification of this organism, with characteristic black chlamydospores, as *P. eupyrena* Sacc. is open to question, and the pathogenicity of the species to potato tissue also remains doubtful.

The culture of *P. solanicola* received from Baarn did not provide sufficient data to allow a direct comparison of this fungus with the cultures of *P. tuberosa* and *P. foveata*, but a comparison was possible using fresh isolates from haulms and information from the literature. In considering the data available, it is apparent that they do not provide a series of differential criteria for the three species, but that they form a satisfactory basis for considering the species as one. The tuber parasites, *P. tuberosa* and *P. foveata*, were found to be pathogenic towards potato stems; therefore, the separation of *P. solanicola*, based on its occurrence on stems, must be considered invalid. Proof of the pathogenicity of fresh isolates from tubers towards stems, and vice versa, also confirms this. The separation of *P. foveata* on the basis of the presence of a pseudo-subiculum must also be considered invalid since there is evidence of a similar structure being present in *P. tuberosa*. Therefore, no single diagnostic criterion is available to separate the three species. The mycelial, pycnidial and spore characteristics of the three species are identical, but the sole criterion not uniformly present is the production of a diffusible pigment as in *P. tuberosa* and *P. foveata*. However, variations in pigment production, observed in the monospore isolations of the latter and in the nutritional studies, and the segregation of colonies observed in *P. tuberosa*, indicate that the production of pigmen cannot be accepted as a specific taxonomic criterion.

It is suggested that the available data confirm the view that *P. solanicol* and *P. tuberosa* are one species and that, with them, *P. foveata* should be included. Therefore, the oldest name of the fungus, *P. solanicola* Prill. & Delacr. sensu Köhler, should be adopted.

Part of this work was carried out during tenure of a Research Studentship from the Agricultural Research Council. Grateful acknowledgement is due to Dr Malcolm Wilson, University of Edinburgh, and Dr Noel F. Robertson, University of Cambridge, for supervision. The opportunity to study the American isolates arose during the tenure of a grant for research at the Maine Agricultural Experiment Station.

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EXPLANATION OF PLATE 22

Fig. 1. Pycnidia of fungus referred to *Phoma tuberosa* on potato tuber.
Fig. 2. Pycnidia of *P. solanicola* on potato stem. × 78.

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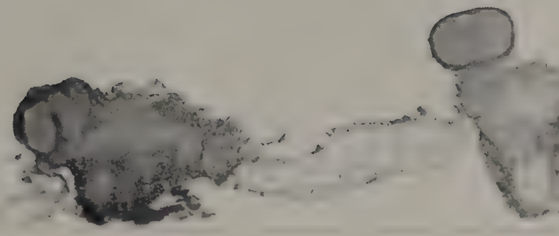

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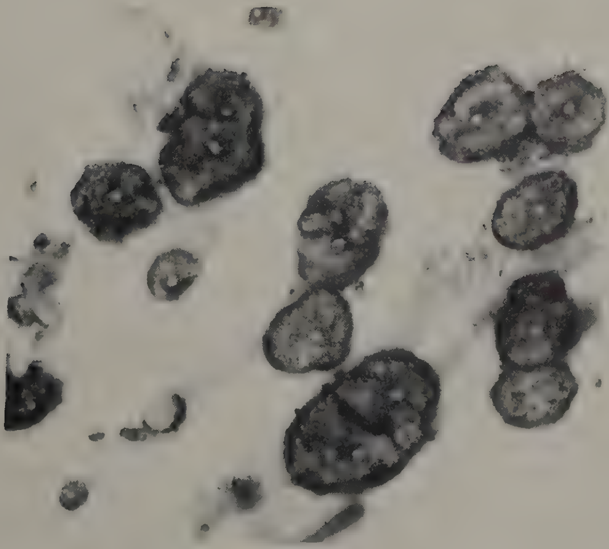

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Trans. Brit. mycol. Soc. **41** (4), 419–445 (1958).

NEW OR INTERESTING RECORDS OF BRITISH HYMENOMYCETES. II

By DEREK A. REID
Royal Botanic Gardens, Kew

(With Plates 23 and 24 and 28 Text-figures)

Descriptions are given of twenty-two hymenomycetes, of which sixteen are new records for the British Isles. The remaining species are included either because of rarity or on account of noteworthy features. Five new species, *Omphalina obscurata*, *Coprinus saichiae*, *Lepiota ventriosospora*, *Sparassis simplex* and *Clavaria lithocras* are described.

The present paper is an attempt to describe some of the interesting collections which have recently been added to the Kew Herbarium. Some of these have been collected by myself, but many were sent by correspondents. It is to these numerous people that I wish to express grateful thanks.

Colour terms in inverted commas are from Ridgway's *Color Standards and Color Nomenclature*, 1912.

AGARICALES

TRICHOLOMATACEAE

LYOPHYLLUM FAVREI (Haller & Haller) Haller & Haller, in *Schweiz. Z. Pilzk.* **28** (4), 49–54, 1950 (Pl. 0, fig. 2; Text-fig. 7).

Synonym: *Tricholoma favrei* Haller & Haller in *Schweiz. Z. Pilzk.* **27** (9), 132–133, 1949.

Cap 7 cm., convex, greyish purple, with dry surface of innate radiating hyphae giving a faint reticulum of darker loose lines under a lens. *Gills* yellow, drying 'Light Brownish Olive', free. *Stipe* 5 cm. long, 1·8 cm. wide, subequal, greyish with purple tint, apex white scurfy. *Flesh* yellowish under the cuticle but salmon pink above the gills and at the apex of the stem, becoming greyish in the stipe. *Smell* not distinctive. *Spores* hyaline, ovate or broadly elliptical, non-amyloid, 3·5–4 × 2·5–3 μ. *Basidia* 4-spored, clavate, 18·2–25 × 5 μ. *Cystidia* none.

Habitat in litter beneath a large beech tree at the Mickleham end of the Druids Grove, Boxhill, Surrey, coll. W. J. Finnigan, 23 Oct. 1956. The collector also stated that this fungus was seen 'some little distance away in 1955' by Mr W. H. Speadbury.

The presence of carminophilous granules in the basidia of this collection has kindly been confirmed by Dr F. B. Hora.

Omphalina obscurata Reid sp.nov. (Text-fig. 5).

= *Omphalia obscurata* Kühner [nomen nudum], in *Ann. Univ. Lyon*, **130**, 1949.

Pileus 0·35–0·7 cm., convexus tandem umbilicatus, hygrophanus, fusco-griseus, griseo-brunneus, vel fusco-sepiaceus, margine involutus leviter pellucido-striatus. *Lamellae* fusco-griseo-brunneae, distantes, latissimae, decurrentes. *Stipes* usque ad 0·8 × 0·1 cm., pileo concolor. *Sporae* hyalinae, late ellipticae, 8·5–11·5 × 5–6 μ. *Basidia* hyalina, clavata, quadrispora, usque ad 26 μ longa, 6–7·5 μ lata. Cystidia nulla.

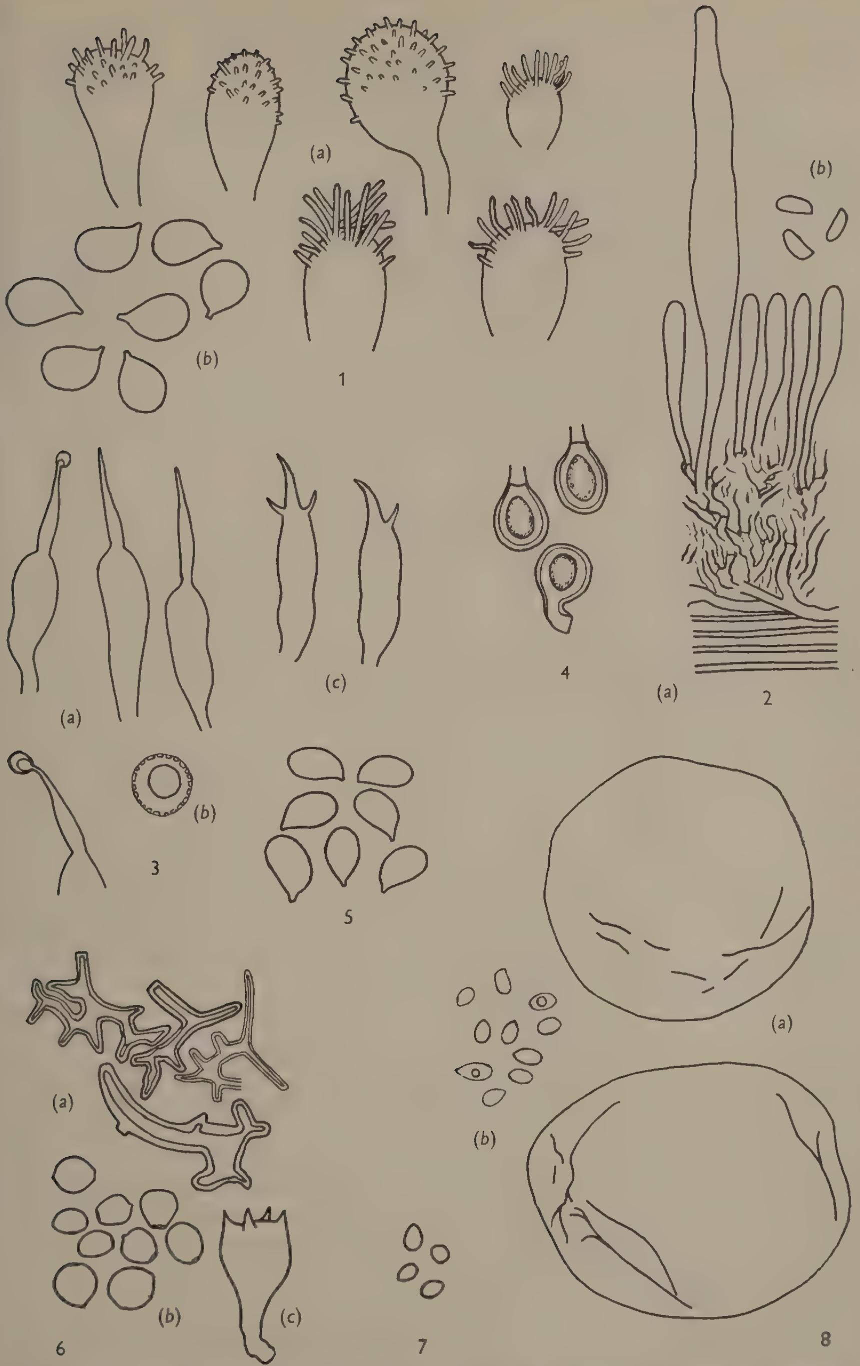
Cap 0·35–0·7 cm., convex or flattened becoming depressed in the centre, dark grey or greyish brown to dark brownish bistre, with faintly striate incurved margin, hygrophanous, drying paler. *Gills* dark greyish brown, distant, very broad, decurrent. *Stipe* up to 0·8 × 0·1 cm., concolorous with the cap, base often covered by white radiating strands of hyphae which run out over the soil forming a small disc of mycelium. *Spores* hyaline, broadly elliptical with prominent lateral apiculus, 8·5–11·5 × 5–6 μ, when measured from a spore print. When spores were examined by mounting a portion of the gill in 10 % potassium hydroxide they appeared very variable in shape —many being subcylindrical or subfusoid—and measured 7·5–11·5 × 4–5·5 μ. *Basidia* hyaline, clavate, 4-spored, up to 26 μ in length, and 6–7·5 μ wide. *Cystidia* absent. *Surface of the cap* formed of several layers of hyphae, 3–15 μ wide with clamp connexions at the septa. These hyphae appear brown owing to the presence of an encrusting pigment which tends to occur in narrow transverse bands. Similar encrusted hyphae are present in the flesh, although the pigment is rather more scattered. *Gill structure* consists of a central pale trama of densely compacted hyphae which appear hyaline or very pale brownish, depending on the amount of encrusting pigment present, flanked on either side by a conspicuous dark-brown subhymenial layer from which the basidia arise.

Habitat growing on a burnt patch of soil amongst *Sphagnum*, Loch Moy, Inverness-shire, coll. D. A. Reid, 28 Aug. 1955 [Typus].

Lange (1955) has observed that the cap of this species may be finely and inconspicuously scaly, and that these scales are minutely pointed in young specimens. He has also found that the stems of young sporophores are clad with short dark hairs. In the same paper he wrote 'The species is truly belonging to the most typical elements in the arcto-alpine flora', and added that 'It is, however, also of common occurrence on poor soil in lowland areas in N. Europe and N. America'.

Kühner & Romagnesi (1953) cite Bresadola (1928), pl. 262, fig. 2, of *Omphalia reclinis* forma *minor* and pl. 262, fig. 3, of *O. rustica* as representing the present species. Whilst the latter figure may well portray *Omphalina obscurata*, it is doubtful if Bresadola's figure of *Omphalia reclinis* forma *minor* can be held to do likewise, as the spores of this taxon were said to be 6–7·5 × 4–4·5 μ, and the hyphae were shown without clamp connexions. Lange (1955) regarded *O. rustica* sensu J. E. Lange as being synonymous with *Omphalina obscurata*, but again the spore size of the former (6·5–7·5 × 4·75–5·5 μ) does not support this view.

The name *Omphalia obscurata* was first published as a *nomen nudum* by Kühner. This illegitimate name is, however, becoming increasingly used in mycological literature, and since there has been no indication that the original author intends to validate the species, I have been forced to do so. It must be noted that Lange (1955) had already recognized the true affinity of *Omphalia obscurata* as published by Kühner, when he transferred it to the genus *Omphalina*.



Text-figs. 1–8. Text-fig. 1. *Mycena megaspora*: (*a*) cheilocystidia; (*b*) spores. Text-fig. 2. *Lentinus adhaerens*: (*a*) section through a gill showing a pleurocystidium; (*b*) spores. Text-fig. 3. *Fayodia bisphaerigera*: (*a*) monosporous basidia; (*b*) spores (both from the Glasgow collection); (*c*) bisporous and trisporous basidia (from the Dunkeld collection). Text-fig. 4. *Lentinellus cochleatus*: chlamydospores. Text-fig. 5. *Omphalina obscurata*: spores (from the type). Text-fig. 6. *Coprinus saichiae*: (*a*) hyphae forming the veil; (*b*) spores; (*c*) basidium (all from the type). Text-fig. 7. *Lyophyllum favrei*: spores. Text-fig. 8. *Lepiota eriophora*: (*a*) cells forming the scales on the cap; (*b*) spores (both from the Bridgwater collection). All ×866.

LENTINELLUS COCHLEATUS (Pers. ex Fr.) Karst., in *Bidr. Finl. Nat. Folk.* **32**, 247, 1879 (Pl. 23, fig. 1; Text-fig. 4).

Synonym: *Lentinus cochleatus* (Pers. ex Fr.) Fr., in *Syst. Orb. Veg.* p. 78, 1825.

This agaric is widespread in the British Isles, and numerous accounts of its morphology and structure have been published by British and continental mycologists. However, examination has shown that this species produces globose to subglobose, brown, terminal or rarely intercalary chlamydospores, 8–13 μ in diam., which are confined to the subhymenial tissues. These structures do not seem to have been recorded for this, or any other, species of *Lentinellus*.

LENTINUS ADHAERENS (Alb. & Schw.) Fr., in *Epicrisis*, p. 391, 1836 (Text-fig. 2).

Synonyms: *L. pulverulentus* (Scop.) Fr., in *Epicrisis*, p. 391, 1836.
L. resinaceus (Trog) Kalchbr., in *Ic. Hym. Hung.* **3**, 47, t. 21 f. 3, 1875.

Cap 2·5–5·5 cm., convex or flattened becoming infundibuliform, pulverulent, whitish then ochraceous cream finally ochraceous, covered with a sticky amber coloured resinous substance, which on drying forms an almost laccate crust; margin indistinctly grooved. *Gills* pale cream, distant, broad (–5 mm.), unequal, decurrent, continued down the stem as distinct lines which are eventually obscured by the tomentum; gill edge coarsely serrated, appearing minutely tomentose under a lens and beaded with resinous droplets. *Stipe* 2–5 cm. long, 0·5–1·1 cm. wide, central or excentric, covered by a whitish or cream-coloured tomentum matted together by a brownish resinous secretion. *Spores* hyaline, cylindrical, non-amyloid, 6–8 × 2–2·5 μ (as measured from dried material). [The spore size of this species is usually given as 6–10 × 2·5–3 μ.] *Basidia* 26–30 × 3·5–4 μ, clavate with four short sterigmata. *Pleurocystidia* projecting above the basidia as obtuse subcylindrical bodies up to 8 μ wide, with thin or very slightly thickened walls. *Smell* sweetish.

Habitat on pine, Cotterill Clough, Ringway, Cheshire, coll. B. Harthan, 1 Dec. 1955.

The gill trama of this fungus consists of parallel hyphae (–5 μ wide) with clamp connexions at the septa. These are thick-walled except toward the gill edge which is formed of the thin-walled, often slightly diverging hyphal endings. There are well-developed subhymenia, 30 μ in thickness, consisting of much-branched thin-walled hyphae 1·5–2 μ in diam. It is from these zones that the basidia and pleurocystidia arise. The latter organs, which never become very thick-walled, should not be regarded as metuloids as has been suggested (Singer, 1951).

Berkeley (1836) wrote of this fungus: 'In very shady woods and plantations Sept.-Oct. Red Rock Plantations, Edgbaston, *Withering*. Ragley Wood, *Purton*.' (Both these records were originally published as *Agaricus adhaesivus* With.) Later (1860) he stated; 'The citation of Withering is doubtful, as he says nothing as to the substance on which his plant grows, though his description corresponds', but made no mention of Purton's record. However, Purton (1821) described his fungus as resembling *Ag.*

eburneus, *nitens* and *nemoralis* of Withering and added: 'It is one of those, which, like many others, can hardly be preserved in a dried state.' From this description the inference is that the fungus was a fleshy terrestrial agaric—almost certainly a species of *Hygrophorus* near *H. olivaceo-albus* or *H. dichrous*. These early records can therefore be rejected, but Berkeley & Broome (1871) listed a collection of *L. resinaceus*—'Forres, M. Terry'—which Stevenson (1879, 1886) compiled as *L. adhaerens* var. *resinaceus*. The description of this collection, which is preserved at Kew, certainly agrees with that of *L. adhaerens*. However, microscopic examination of sections through the gills failed to reveal the characteristic cystidia, showed much less well-developed subhymenia, and thin-walled tramal hyphae. Berkeley & Broome (1876) described a collection of *L. pulverulentus* [Glamis, Hunters Hill, J. Stevenson, 1875] which was compiled by Stevenson (1879), who also listed an additional collection of *L. adhaerens* [Balnamoon, Rev. M. L. Anderson]. There is material in the Kew Herbarium labelled '*L. pulverulentus*, Menmuir, Anderson' by Berkeley, which is very probably the same as the Anderson gathering cited as *L. adhaerens* by Stevenson. This collection, which has abundant chlamydospores in the subhymenium, strongly amyloid subglobose spores, and gloeocystidia arising from oleaginous hyphae in the trama, is *Lentinellus cochleatus* (Pers. ex Fr.) Karst.

As the old records of *L. adhaerens* appear to be so unreliable, they are best rejected. The first authentic collection of the species from this country would then seem to be the Cotterill Clough material described above.

FAYODIA BISPHAERIGERA (Lange) Singer, in *Ann. mycol., Berl.*, **34**, 331, 1936 (Text-figs. 3, 27).

Synonyms: *Omphalia bisphaerigera* Lange, in *Fl. Agar. Dan.* **2**, 56, 1936.
Mycena bisphaerigera (Lange) A. H. Smith, in *North American Species of Mycena*, p. 449, 1947.

Cap 2·4 cm., convex becoming flattened and slightly depressed, hygrophanous, grey-brown with strongly striate margin, drying pale dirty brownish or fawn from the centre outwards. In young sporophores the disc has a distinctly mealy appearance owing to the presence of separable silky fibrils. *Gills* distant, broad (–5 mm.) adnate or emarginate, sometimes with a conspicuous decurrent denticle, grey. *Stipe* usually long and thin [sometimes rather short and stout (4 × 0·4 cm.)], hollow, glabrous, pruinose at the apex, pale grey. *Flesh* concolorous with the cap. *Spores* hyaline, spherical, amyloid, 7–11 μ, with an almost wheel-like appearance. Kühner (1930) has described the spores of this species, under the name *Omphalia striaepilea* sensu Ricken, as having 'une membrane triple composée d'une épispore lisse et amyloide et de deux autres membranes non amyloides: une mésospore ornée et une endospore lisse bien distincte'. *Basidia* 20·8–33·8 × 6–9 μ, with one, two or three sterigmata. *Cheilocystidia* seen only in the Inverness-shire collection, as long, thin-walled, clavate to more or less cylindrical structures with swollen bases. They are somewhat often constricted and may narrow towards their obtuse apices. In some of the sporophores of this gathering the larger cheilocystidia, which reach 90 μ in length, develop a clamped septum near the base. This is an extremely unusual feature in the Agaricaceae, although such cystidia are of common occurrence in the Thelephoraceae. Favre (1948) describes the cystidia 'à parois minces, pédonculées, claviformes ou plus souvent ventrues dans leur partie inférieure et terminées par un appendice de longueur variable; elles mesurent 36–90 × 10–18 μ', in *Fayodia bisphaerigera* var. *bisphaerigera*. *Habitat* in coniferous wood, Dunkeld, Perthshire, coll. D. A. Reid, 23 Aug. 1953; on bare soil on the side of a deep ditch in a beech wood, near Glasgow, Lanarkshire, coll. R. H. Johnstone; amongst moss and grass, Dougalston, Stirlingshire, coll. R. H. Johnstone, 30 Sept. 1956; under spruce, road from Loch Morlich to Loch Pityoulish, Inverness-shire, coll. D. A. and P. M. Reid, 15 September 1957.

This species, which was first collected in Britain in 1953 (see *Trans. Brit. mycol. Soc.* **37**, 186, 1954), is of particular interest on account of its basidia. As indicated above these may be either 1-, 2-, or 3-spored, and Singer (1951) has stated that there is a 4-spored form of *Omphalia bisphaerigera*. However, whilst the Dunkeld collection shows basidia with one, two and three sterigmata, the basidia of the Glasgow gathering are almost all monosporous. Some of the basidia of the Dunkeld material are quite typically two-spored, but others produce one main sterigma and a much smaller one. The trisporous basidia nearly all produce one main sterigma and two smaller often unequal ones. These small sterigmata have been observed to bear spores—in some instances at least—although it is not known whether they develop to maturity. The monosporous basidia produce one very large terminal sterigma up to 20·8 μ in length, and 3 μ in width at the base. It seems that there is a tendency in this species towards the reduction of the number of sterigmata per basidium, culminating in the monosporous state.

MYCENA MEGASPORA Kauffman, in *Pap. Mich. Acad. Sci.* **17**, 182–183, 1933 (Text-fig. 1).

Synonym: *M. uracea* Pearson, in *Trans. Brit. mycol. Soc.* **22**, 32–33, 1938.

Cap 1 cm., markedly campanulate, rivulose, blackish brown. *Gills* whitish, ascending, subsinuate, thin, broad, rather distant. *Stipe* 3 cm. long, smooth, slender, firm, whitish brown, darker toward the base which is prolonged into a tapering pseudorhiza. *Spores* hyaline, amyloid, broadly elliptical or pip-shaped, with prominent lateral apiculus, (8–)10–13(–14) × 6–8 μ. *Basidia* clavate, 31·2–39 × 7·5–8·5 μ, with 2 or 4 large sterigmata up to 13 μ long and 3·5 μ wide at the base. *Cheilocystidia* abundant, very variable in size and shape, from subcylindrical to subspherical, the obtuse apices either densely or sparsely covered with short or long finger-like processes. *Pleurocystidia* absent. *Pileus trama* consisting of a thin pellicle of very narrow hyphae, covered with numerous minute projections, beneath which is a narrow layer formed of slightly enlarged hyphal elements with brown contents, followed by a broad zone of densely compacted hyphae staining deeply in aniline blue in lactic acid. The latter zone is continuous with the central strand of the gill trama, where it is flanked on either side by a subhymenium up to 15·6 μ wide, formed of parallel hyphae which do not show very great affinity for the above-mentioned stain.

Habitat on peat, Killakee Mountain, Dublin, Eire, coll. F. C. Hassell and W. Allen, 17 Oct. 1955.

Pearson (1943) wrote of *M. uracea*: 'Since this species was recorded, R. Kühner's Monograph of the genus *Mycena* has been published, and he describes, under the name *M. megaspora* Kauffman, an American species which may be identical with *M. uracea*. The habitat is different; *M. megaspora* is found on bare peaty soil, while *M. uracea* appears on burnt ground attached to the roots of heather.' He added that: 'Until further observations are made *M. uracea* can stand.' Kühner & Romagnesi (1953) retained *M. uracea* as a distinct species and separated it from *M. megaspora* on habitat and spore size. However, Lange (1955), writing of *M. megaspora*, stated: 'I fail to find any consistent difference between this species and *M. uracea* Pearson...etc.' He gave the spore size of a form with 2-spored basidia as 11–14·2 × 7·1–8·7 μ and of a 4-spored form as 9·0–12·8 × 6–7·2 μ; he also noted that the species was common in *Empetrum* vegetation, and that it was probably attached to the roots of this shrub.

In the author's opinion the specimen described above supports Lange's view that there are no specific differences separating *M. uracea* and *M. megaspora*, and the former has therefore been listed in synonymy. The range of spore size of the Eire specimen includes that of both *M. uracea* and *M. megaspora*. Further, this specimen was growing, in peat, with other sporophores referable on spore size alone (9 × 6 μ) to *M. uracea*; the structure of the pileus and gill trama of both 'species' is also identical.

AMANITACEAE

PLUTEUS MINUTISSIMUS R. Maire, in *Fungi Catalaunici*, p. 94, 1937 (Text-figs. 13, 28).

Synonym: *P. psichriophorus* (Berk. & Br.) Sacc. var. *minutissimus* (Maire) Singer in *Trans. Brit. mycol. Soc.* **39**, 214, 1956.

Cap 1·1 cm., convexo-plane, with an obtuse central umbo seated in a depressed zone, velvety, dark brown, almost black at the umbo. *Gills* free, crowded, rather broad, ventricose, obtuse at the margin, pink. *Stem* 1·6 cm. long, 0·1 cm. wide at the base, attenuated upward, pale brown, darker at the base. *Spores* pale flesh coloured, broadly elliptical, monoguttulate, 5–7·5 × 4–5 μ. *Basidia* 16–23·4 × 6–8 μ, 4-spored, pedunculate, expanded above but contracted beneath the sterigmata, which are borne at the apex of a short ill-defined neck. *Cheilocystidia* subspherical, pedunculate, hyaline, with heads 14–26 × 12–20·8 μ. *Pleurocystidia* not seen in either the fresh or dried material, although sections through the gills of the exsiccatum show a number of vesicular gaps in the hymenium which may have been caused by collapsed cystidia. *Surface of the cap* formed of two types of thin-walled cells with brown contents (*a*) subspherical, pyriform or ovate, pedunculate, 15–33·8 μ in diameter, (*b*) elongate-lanceolate, up to 150 μ long and 20·8 μ wide; elements intermediate in shape also occur. *Surface of the stem* covered, at least at the base, with very elongated, obtuse, subcylindrical, thin-walled hairs with brown contents.

Habitat on *Buxus*, Belton Park, Grantham, Lincs, coll. Miss G. M. Waterhouse, 22 Oct. 1955.

The fungus described above agrees well with the description of *P. minutissimus* given by Favre (1948), differing only in habitat, the slightly narrower spores, somewhat smaller basidia, subspherical cheilocystidia, and in the possible absence of pleurocystidia.

Kühner (1956) has also given an account of this species and has described a forma *major* which appears to differ from forma *minutissimus* (erroneously referred to as forma *typicus*) in growing on stumps instead of being strictly terrestrial, in its larger size, larger basidia, and in having numerous elongated hairs with brown contents on the stipe (at least in the basal region), but he admits that there is a scale of intermediates connecting these two forms. The above collection differs from forma *major* in much the same way that it differs from the account of *P. minutissimus* given by Fayre and additionally in its smaller size. It would, therefore, appear to belong to the intermediate series connecting forma *minutissimus* and forma *major*, although the value of these taxa is questionable.

Since describing the specimen cited above an additional sporophore has been collected and an account of this has been included as it is better preserved.

Cap 0·7 cm., convex, velvety, dark brown. *Gills* as above. *Stem* 0·9 × 0·15 cm. greyish hyaline, densely but very minutely pubescent under a lens except for the apex. *Spores* subglobose to very broadly elliptical, monoguttulate, 5–7·5 × 4·5–6 μ. *Basidia* as above but larger, 26–31·2 × 6–7·5 μ. *Cheilocystidia* 12–56 × 9–20 μ, very variable in both size and shape, from subspherical to clavate, obovate or rarely subcylindrical, pedunculate, hyaline or with very pale brown contents. *Pleurocystidia* abundant, mostly obovate, 40 × 19 μ. *Surface of the cap* formed of two types of cells as above. *Surface of stem* covered by caulocystidia. In the basal region these are elongated, obtuse, subcylindrical, thin-walled organs, with brown contents, but higher up they may be lanceolate, clavate or spherical.

Habitat growing on the site of a fire on bare soil, Great Brickhill, Bletchley, Bucks, coll. D. A. Reid, 27 Oct. 1957.

AGARICACEAE

LEPIOTA ERIOPHORA Peck, in *Bull. Torrey bot. Cl.* **30**, 95, 1903 (Pl. 24, fig. 4; Text-fig. 8).

Cap 2·8–2·9 cm., convex, sometimes with a slightly elevated central disc, the cuticle disrupting into minute conical dark brown scales on a pinkish buff coloured background except at the centre. *Gills* unequal, crowded, whitish, free. *Stipe* up to 6 cm. long, and 0·5 cm. wide, white at the apex, becoming pinkish and finally pinkish buff towards the slightly enlarged base which is covered with dark brown scales. There was no ring on any of these specimens, although a woolly ring is apparently normally present. *Spores* hyaline, elliptical, 4–5(–6) × 2–3 μ, often adhering in groups. *Cystidia* absent. *Scales of the cap and stipe* formed of brown, thin-walled globose to subglobose cells 25–65 μ in diam., which tend to collapse rather readily.

Habitat in a wood consisting mainly of hazel (*Corylus*) and silver birch

Betula) with a few beech trees (*Fagus*), Higher Merridge, Bridgwater, Som., coll. Mrs E. A. Marriage, 22 Aug. 1956; Frithsden Beeches, Berkhamsted, Herts, coll. Mrs P. M. Reid, 13 Oct. 1957.

Lepiota ventriosospora Reid, sp.nov. (Pl. 24, fig. 3; Text-fig. 9).

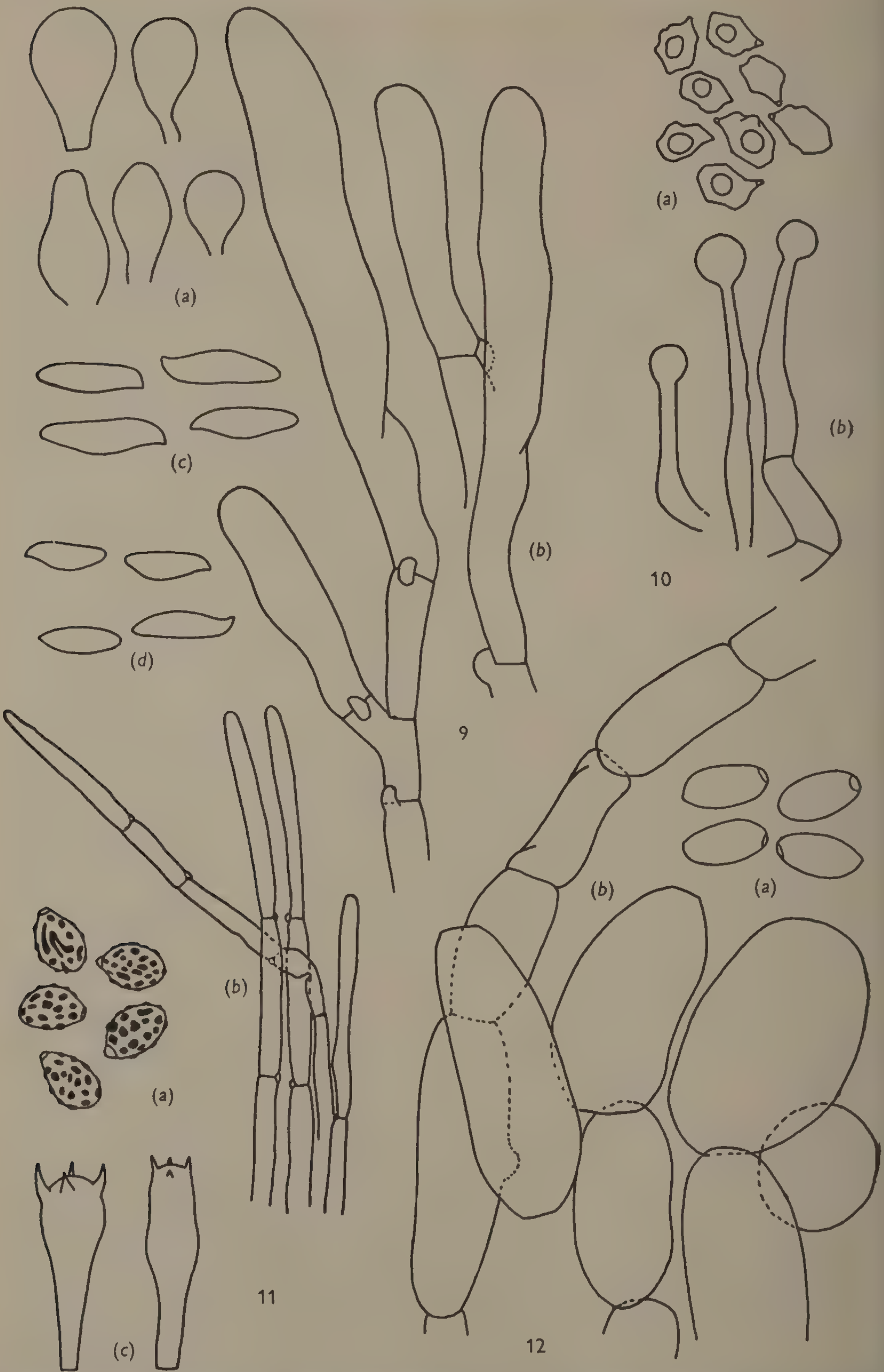
Synonym: *L. metulaespora* (Berk. & Br.) Sacc. sensu Bres., in *Iconographia Mycologica*, **1**, Tab. 30, 1927.

Pileus 2·5–5·5 cm., convexus, plus minusve gibbosus vel umbonatus, squamis fusco-brunneis dense obsitus, centro laevis. *Lamellae* albae, inaequales, confertae, postice liberae. *Stipes* 6–10 cm. longus, 0·5–1·2 cm. latus, cavus, pallidus, infra annulum squamulis rubello-brunneis vel citrinis obtectus, saepe ad basim lineis fusco-brunneus subspiraliter ornatus. *Caro* pilei alba, stipitis fuscescens. *Sporae* hyalinae inaequaliter ventricosae, 13–20·8 × 4–5 μ. *Cheilocystidia* 9–15 μ lata, ovata vel obovata. *Cuticula* pilis unicellulis, usque ad 468 μ longis, 10–18 μ latis composita.

Cap 2·5–5·5 cm., convex, more or less umbonate, the cuticle disrupting, except round the dark brown umbo, into small brown tile-like fibrillose scales on a brownish fawn base with a pinkish or pinkish orange tinge; margin appendiculate with the remnants of the thick, felty, yellowish or pinkish brown veil. *Gills* unequal, crowded, whitish, free. *Stipe* 6–10·5 cm. long, 0·5–1·2 cm. wide, hollow, slightly narrowed towards the pallid apex, densely covered by the thick woolly yellowish or pinkish brown veil, beneath the cottony evanescent annulus, and sometimes bearing dark brown raised felty more or less spiral bands on the basal portion. *Flesh* whitish in the cap, brownish in the stipe of older specimens. *Spores* hyaline, mummy-shaped, 13–20·8 × 4–5 μ. The shape of the spores can best be described by drawing an analogy between them and the profile of a rather corpulent human figure. *Cheilocystidia* 9–15 μ wide, variable in shape from obovate to ovate. *Surface of the cap* formed of very long cylindrical unicellular hairs with rounded or more rarely slightly narrowed or even obtusely pointed apices. These hairs may be up to 468 μ in length, and 10–18 μ in width, and arise from brown septate hyphae to which they are joined by a clamp connexion. They themselves are brown at the base but become hyaline towards their free extremities.

Habitat growing under fir trees, Higher Merridge, Bridgwater, Som., coll. Mrs E. A. Marriage, 10 Oct. 1955; on grass verge under mixed trees, Ashridge, Herts, coll. D. A. Reid, 15 Oct. 1955 [Typus]; Manby Wood, Broughton, Lincs, coll. Miss G. M. Waterhouse, 13 Oct. 1956. [The species has also been reported from Murthley Castle Estate, near Dunkeld, Perthshire, *Trans. Brit. mycol. Soc.* **37**, 186, 1954.]

L. ventriosospora is very closely related to *L. metulaespora*—a species originally described from Ceylon—but the latter differs in having a white veil and in being constantly sulcate half-way to the centre, thin fleshed, and much less robust. The microscopic structure of both species is very similar. The type specimens of *L. metulaespora* (Thwaites no. 1180) have a cuticle formed of long cylindrical unicellular obtuse hairs which are hyaline throughout, and mummy-shaped spores 11–17 × 4–5 μ. Petch (1917) has given an excellent account of this species which is reproduced below 'Pileus 2·5–4 cm. diameter, broadly campanulate, obtusely umbonate, umbo yellow-brown or reddish brown, smooth, elsewhere clothed with



Text-figs. 9-12. Text-fig. 9. *Lepiota ventriosospora*: (*a*) cheilocystidia (from the type); (*b*) hairs from the surface of the cap (from the Bridgwater collection); (*c*) spores (from the type); (*d*) spores from the type of *L. metulaespora*. Text-fig. 10. *Eccilia molluscus*: (*a*) spores; (*b*) hairs from the stipe. Text-fig. 11. *Coprinus insignis*: (*a*) spores; (*b*) cells forming the veil; (*c*) basidia. Text-fig. 12. *Coprinus flocculosus*: (*a*) spores; (*b*) cells forming the veil. Text-fig. 10. (*b*) ×400; others, ×866.

concentrically arranged, thin, floccose, pale brown to whitish, adpressed scales and warts, white and silky fibrillose under the scales, sulcate half-way to the centre; margin symetimes appendiculate; flesh white, thin. Stalk 6–8·5 cm. high, 3 mm. diameter, slightly swollen at the base, strongly fibrillose with longitudinal white fibrils, yellowish and glabrous when the fibrils are rubbed off, hollow, turning yellow-brown internally when cut, lined with shining white fibrils. Gills white, free, ventricose, broad, rounded at both ends. Spores white, 2–6 guttulate, fusiform, ends pointed, or sigmoid on one side, 15–18 × 6–7 μ.' Despite some similarities in microstructure, comparison of dried material of the two species shows them to be questionably distinct.

L. ventriosospora (under the name *L. metulaespora*) has been much confused with *L. clypeolaria* (Bull. ex Fr.) Kummer, from which it can at once be distinguished by the shape of its spores [see Kühner (1936), fig. 8, nos. 30, 31 and 32]. In addition, the latter species tends to be less robust, and has the cuticle of the pileus disrupting into minute brown scales on a whitish background. The colour of the veil of the present species, generally described as yellowish, has been used as a diagnostic character in the separation of *L. ventriosospora* from its allies. However, the colour of the veil, although considerably darker than in *L. clypeolaria*, varies from yellowish to pinkish brown.

The name *L. metulaespora* has appeared in works on British mycology since Berkeley & Broome (1871) in their original description of the species from Ceylon stated: 'This agrees, as to the spores, with no. 6447 from Alabama, which is apparently a form of the same species, which occurs also in England.' This sentence is somewhat ambiguous, but has generally been taken to mean that *L. metulaespora* occurred in this country. If in fact Berkeley & Broome really meant that it was the Alabama form which grew in Britain, the situation becomes rather different, for this specimen preserved at Kew is quite distinct from the Ceylon fungus. It lacks the sulcate pileus, has differently shaped spores, and may possibly be *L. clypeolaria.* It was probably because of Berkeley & Broome's statement, quoted above, that Bresadola adopted the name *L. metulaespora* for his European specimens. There is no evidence to show that the records of this species cited by Cooke and Massee refer to *L. ventriosospora.* Rea (1922) stated: 'The records of this (*L. metulaespora*) as British are erroneous; they should be referred to *Lepiota clypeolaria* (Bull.) Fr. as defined above.' Pearson & Dennis (1948) omitted it from their list of British Agarics.

COPRINACEAE

COPRINUS FLOCCULOSUS (DC. ex Fr.) Fr. sensu Romagnesi, in *Rev. Mycol., Paris*, **10**, 83–86, 1945 (Text-fig. 12).

Synonym: *C. rostrupianus* E. C. Hansen sensu Lange, in *Fl. Agar. Dan.* **4**, 109–110, pl. 157E, 1939.

Cap 2·0 cm. high, conical then expanded and flattened sulcate almost to the disc, ivory-white, covered by the floccose veil which disrupts into rather thick pure white granular fragments. *Gills* free, black, deliquescent. *Stipe* 11 cm. long, 0·5 cm. wide at the base, attenuated upwards, hollow, white, polished. *Spores* blackish brown, elliptical, 11–18 × 6–9 μ, with an oblique germ-pore. *Cystidia* not seen, but Romagnesi (1945) describes the pleurocystidia as 'globuleuses ou elliptiques, 65–115 × 28–65 μ' and the cheilocystidia as 'subglobuleuses, 20–65 × 35–65 μ'. *Veil* formed of branching chains of thin-walled cells ranging from cylindrical to broadly ovate, and even globose, 17–54 × 5–26 μ.

Habitat growing in sandy soil of path much used by horses, Esher Common, Surrey, coll. A. P. L. Digilio, 7 June 1953; growing in soil which had been enriched with compost formed of rotted sawdust and wood chips. Royal Botanic Gardens, Kew, Surrey, coll. D. A. Reid, 3 Apr. 1957.

C. flocculosus has been recorded by Berkeley & Broome (1861, 1883) from King's Cliffe, Northants, 1860, and Cooke (1881–91) has reproduced Berkeley's coloured illustration [pl. 654 (667)] of this collection, which is preserved in the Kew Herbarium. However, the spores of this material are dark brown, 13–14 × 8 μ, with an apical germ-pore, and do not match those of *C. flocculosus* sensu Romagnesi. Rea (1922) has also reported this species but he described the spores as 10 × 7–8 μ [although these measurements may well have been taken from Massee (1892)], which is considerably smaller than those of the fungus described above.

COPRINUS INSIGNIS Peck, in 26*th Rep. N.Y. St. Mus.* p. 60, 1873 (Pl. 24, fig. 5; Text-fig. 11).

Cap 4 cm. high, 3·3 cm. wide, campanulate then expanded and flattened, thin, grey, sulcate-striate almost to the pale brown disc, covered with a silky fibrillose veil; margin becoming blackish as the gills deliquesce. *Gills* ascending, free, crowded, black; gill edge entirely separable. *Stipe* 8 cm. long, 0·7 cm. wide, floccose, hollow, very pale brown to almost white. *Spores* dark brown at maturity, amygdaloidal, 9–12(–13) × 6–8(–9·5) μ, with a conspicuous ornamentation of isolated warts and irregular thickenings, and a very prominent, hyaline, apical almost snout-like germ pore. *Basidia* 23–33·8 × 9–10·5 μ, 4-spored, clavate. *Cystidia* not seen, but Kühner (1928) describes them as 'faciales énormes et saillantes, vésiculeuses, mesurant par exemple 80–180 × 60 μ'. *Veil* formed of long chains of cylindrical cells, 52–143 × 8–26 μ, with clamp connexions at the septa.

Habitat caespitose, in a hollow beech stump, Burnham Beeches, Bucks, coll. D. A. Reid, 13 Oct. 1956.

This species looks very much like the common *C. atramentarius* but differs in having a silky fibrillose veil and warted spores. *C. insignis* was recorded from France by Kühner (1928), but there is a collection in the Kew Herbarium determined in error as *C. atramentarius* bearing the following data 'Bois de Boulogne, Oct. 1849'.

Coprinus saichiae Reid, sp.nov. (Text-fig. 6).

Pileus 0·3 cm. altus, 0·2 cm. latus, campanulatus, demum expansus, membranaceus, floccosus, albus, disco saepe cremeo tincto. *Lamellae* nigricantes, subliberae. *Stipes* primo usque ad 0·6 cm. altus, 0·1 cm. latus, demum 2·2 cm. altus, albus. *Sporae* griseo-brunneae, pellucidae, 6–8 × 5–7·5 × 4·5–5 μ. *Basidia* quadrispora, clavata, pedicellata, 20·8–28·6 × 9–11 μ. *Cystidia* non visa. *Velum* hyphis hyalinis, luteo-brunneis, coralloideis, 2–2·5(–6) μ, muris crassis, compositum.

Cap 0·3 cm. high, 0·2 cm. wide, campanulate, at length expanded and flattened with revolute margin, very thin, white, often with a cream tint at the disc, floccose. As the gills deliquesce and the cap expands, the fungus becomes greyish or blackish from the margin inward, sulcate striate, and very diaphanous. *Gills* becoming black, more or less free. *Stipe* at first up to 0·6 cm. high, 0·1 cm. wide, but lengthening rapidly, reaching a height of 2·2 cm., white. *Spores* grey-brown, translucent, subglobose to rather triangular in some planes but elliptical in others, 6–8 × 5–7·5 × 4·5–5 μ, with an apical germ-pore. *Basidia* 4-spored, clavate, pedicellate, 20·8–28·6 × 9–11 μ. *Cystidia* not seen. *Veil* formed of thick-walled, hyaline or yellowish brown, coralloid hyphae, 2–2·5(–6) μ wide.

Habitat growing on dead grass in a lawn, King's Langley, Herts, coll. Mrs. R. A. Saich, 23 Sept. 1955 [TYPUS]; same locality, coll. Mrs R. A. Saich, autumn 1954.

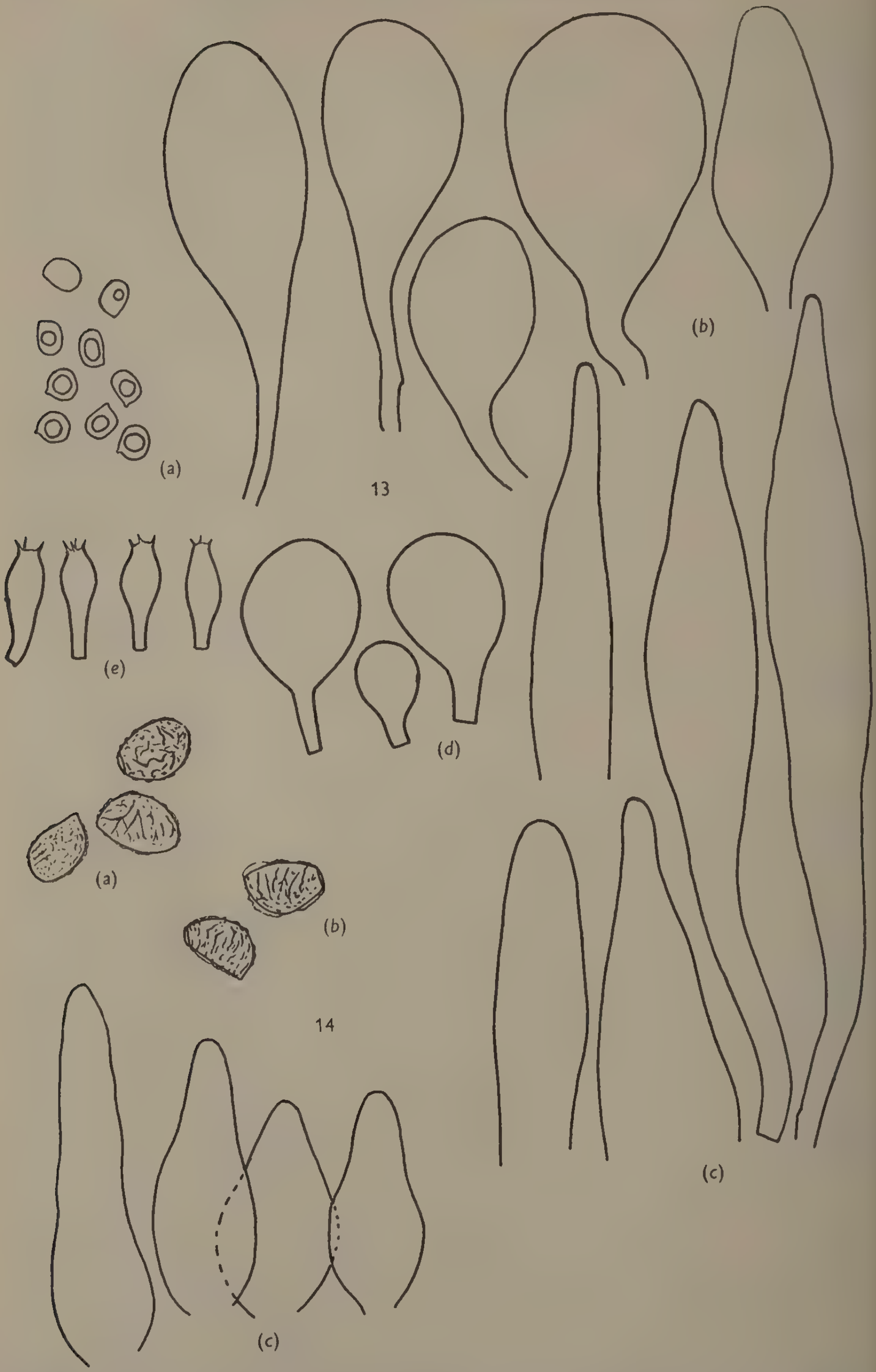
This species is very close to *C. gonophyllus*, from which it can be distinguished by the smaller size, gill shape, veil structure, paler grey-brown spores, and its habitat. Locquin (1955) described *C. picosporus* which is clearly related to *C. saichiae*, but this seems to have larger spores. In the description of his species Locquin gives the spores as '$\frac{10}{8} \times 8\frac{9}{8} \times 7{\cdot}5\ \mu$ globuleuse à courtement amygdaliformes, peu colorées au microscope', and in the Latin diagnosis as 10 × 8 μ. However, his spore drawings (fig. 5) do not agree with these measurements, if, as stated, they are × 2000. Alternatively, if, as appears to be the case in fig. 3, this should read × 1000, then the spores would seem to be 10–12 × 8·5 × 7·5–8·5 μ.

COPRINUS SILVATICUS Peck, in *24th Rep. N.Y. St. Mus.* p. 7, 1870 (Text-fig. 14).

Synonyms: *Coprinellus tardus* Karst., in *Bidr. Finl. Nat. Folk.* **32**, 543, 1879.
Coprinus tardus (Karst.) Karst., in *Finlands Basidsvampar*, p. 266, 1889.

Cap 1·3–2·3 cm. high, 0·8–1·8 cm. wide at the base, ovate then campanulate, at length expanded and more or less convex, sulcate almost to the apex, at first alutaceous with ochraceous disc, or entirely ochraceous, darkening with age to ochraceous-brown. *Gills* adnexed or free, black. *Stipe* up to 8·5 cm. long, 0·2–0·4 cm. wide, white, silky polished, striate. *Spores* amygdaloidal, dark brown or black in potassium hydroxide, 11–15·6 × 7–9·5 × 8–10 μ, with a prominent hyaline, apical snoutlike, germ-pore. The spores have an ornamentation of thickened, irregular, often branched lines, said to be due to the wrinkling of the hyaline epispore, and a crenulated outline. *Cheilocystidia* thin-walled, bottle-shaped, 33·8–65 × 13–26 μ, with the neck variably developed. *Pilocystidia* similar to the cystidia on the gill edge, but larger, up to 90 × 23·4 μ. *Cuticle* cellular.

Habitat on the ground, Royal Botanic Gardens, Kew, Surrey, coll. Lieut. Shuttleworth, 28 Nov. 1945; tufted, Mickleham, Surrey, coll. A. A. Pearson (ex Herb. A. A. Pearson), 25 Oct. 1948; Gomshall, Surrey, coll. P. Orton (ex Herb. A. A. Pearson), 16 Nov. 1951; solitary, on the ground under beeches, Burnham Beeches, Bucks, coll. Mrs P. M. Reid, 14 Oct. 1956.



Text-figs. 13–14. Text-fig. 13. *Pluteus minutissimus*: (*a*) spores; (*b*) subglobose to ovate cells from the cap surface; (*c*) elongate-lanceolate cells from the cap surface; (*d*) cheilocystidia (all from the Belton Park collection). Text-fig. 14. *Coprinus silvaticus*: (*a*) spores (from the Kew collection); (*b*) spores; (*c*) cheilocystidia (both from the Burnham Beeches collection). All ×866.

This species has frequently been listed in continental works as *C. tergiversans* (Fr.) Fr. sensu Ricken, and appears as such (and again as *C. tardus*) in the Pearson & Dennis (1948) list of British Agarics and Boleti. Ricken's (1915) description and plate (pl. 22, fig. 6) of *C. tergiversans* would seem to agree more closely with *C. insignis* Peck than with *C. silvaticus*. He figures a robust, caespitose species, with floccose stipe and coarsely warted spores, although it must be admitted that the colour is not typical of *C. insignis*. The figure may, however, have been based on dried up, sun-scorched material. From an examination of his exsiccati and drawings of *C. tergiversans* preserved at Kew, it is clear that Pearson interpreted this species in the sense of *C. silvaticus* Peck. It is therefore preferable to adopt the latter name for the fungus described above.

RHODOPHYLLACEAE

ECCILIA MOLLUSCUS (Lasch) Quél., in *Mém. Soc. Émul. Montbéliard*, 2e serie, **7**, 334, 1873 (Text-fig. 10).

Synonym: *Agaricus molluscus* Lasch, in *Linnaea*, **3**, 398–399, 1828.

Cap 0·6–1·6 cm., convex then flattened, finally with somewhat raised margin, pure white with a distinct satiny lustre, non-hygrophanous, appearing almost mycenoid. *Gills* distant, at first white then pink, more or less decurrent. *Stipe* 1–3·2 × 0·1–0·13 cm., white, sometimes, tinted yellow in older specimens. *Spores* angular, 9–10·5 × 5·5–6·5 μ. *Cheilocystidia* absent. *Hyphae of the cuticle* of both pileus and stipe bearing long narrow hairs up to 60 μ in length, terminated by globose heads 5–8·5 μ in diameter.

Habitat growing on bare soil in deep shade under beech trees, Frithsden Beeches, Berkhamsted, Herts, coll. D. A. Reid, 2 Oct. 1955.

In Britain this species has in the past been called *Leptonia sericella* (Fr.) Barbier and, in fact, Romagnesi (1939) and Kühner & Romagnesi (1953) cite the Cooke (1881–91) plate [pl. 335 (307)] of *Agaricus* (*Leptonia*) *sericellus* as representing *E. molluscus*.

The correct specific name for this fungus is *molluscus*. Fries in the index to the *Systema* listed *Agaricus molluscus* Lasch, but he erroneously referred to it as *A. molliusculus* in the *Epicrisis* and subsequent works. This error has resulted in the name *molliusculus* being in current use.

It is very questionable if the fungus described above is really the same as that of Lasch, which was described as having the pileus 'campanulato subumbonato margine inflexo-convexus, 1–1¼ unc. latus, floccis densis subfibrillosis innatis, . . .etc.' The description of the stipe 'Stipes 1½–2 unc. longus, 1–1½ lin. crassus, subaequalis, basi parum incrassatus, albofloccosus et fibrillosus', is also hardly applicable. However, whilst doubt exists regarding the use of Lasch's epithet, it is almost certain that the fungus from Berkhamsted is the same as that described by Kühner & Romagnesi (1953) under the illegitimate name *Rhodophyllus molliusculus* (Lasch) Romag.

APHYLLOPHORALES

POLYPORACEAE

Heteroporus biennis (Bull. ex Fr.) Laz., in *Rev. Acad. Madr.* **15**, 119, 1916 (Pl. 23, fig. 2; Text-fig. 15).

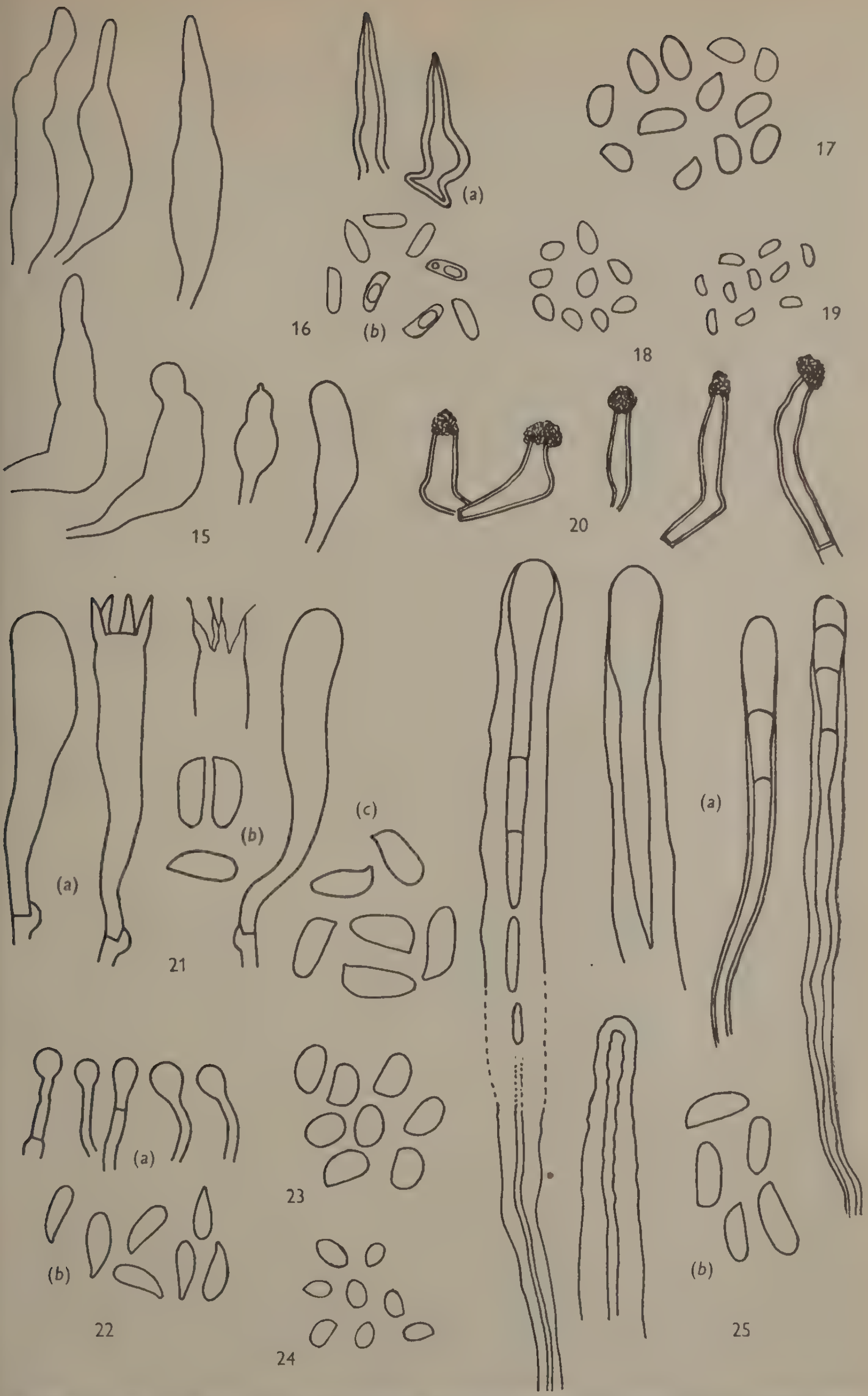
Synonym: *Daedalea biennis* Bull. ex Fr., in *Syst. Myc.* **1**, 332, 1821.

Numerous accounts of this well-known and widespread species have been published, but despite the fact that some European mycologists have given details of the microstructure and have described the formation of chlamydospores in the hymenium, they do not mention the presence of gloeocystidia even though De Seynes (1888) had previously figured them [pl. 6, fig. 10] as a 'réservoir à suc propre'. Bondartsev (1953) actually states that cystidia are absent in this fungus. However, Overholts (1953) observed 'cystidia' in American material. He wrote 'cystidia occasionally present but never abundant, inconspicuous, scarcely projecting beyond the basidia, hyaline, cylindric, usually blunt, 5–10 μ in diameter, sometimes with forked tips', and added: 'The variation in the number and form of the cystidia is unusual. Some collections show only small and relatively inconspicuous cystidia; others have this type and, in addition, a very conspicuous type, often with forking tips.'

The present author has examined eighteen British collections of *H. biennis* and found conspicuous thin-walled, highly refractive gloeocystidia in each. These organs start as small ovate bodies and grow out to form long cylindrical or fusiform structures, which may become rather irregular or variously constricted, especially near the apex. The apical constrictions indicate that the gloeocystidia have undergone periods when their growth was arrested, and have subsequently started to grow again. When renewed growth occurs it may be somewhat excentric and give the impression of branching, but not a single gloeocystidium with a truly forked apex was seen. Overholt's statement that some collections of *H. biennis* had two types of cystidia was probably the result of his having observed mature and initial stages in development of gloeocystidia. These organs arise in the trama of the tube walls and are frequently about 40 μ in length, but may reach 78 μ, and 6–12 μ in width.

Phellinus ferreus (Pers.) Bourd. & Galz., in *Hyménomycètes de France* (Text-fig. 16), p. 627, 1928.

Fructifications forming large resupinate poroid patches, which may extend for up to 48 cm., covering the undersides of living or dead branches. *Pores* 3–4 per mm., round or subangular, with rather thick dissepiments, minutely tomentose under a lens, glancing in the light, and varying in colour from 'Ochraceous Tawny' to 'Hazel', but frequently tinted with 'Pallid Brownish Drab' or 'Pale Brownish Drab'. *Tubes* becoming indistinctly layered in older specimens, so that the fruit-body may exceed 1 cm. in thickness. *Flesh* thin, 'Orange Rufous', blackening when touched with a solution of potassium hydroxide. *Spores* hyaline, subcylindrical, 5–8 × 2–2·5 μ with one or two guttules. *Basidia* hyaline, clavate, 9–11 × 4–5 μ. *Setae* abundant, 18–41·6(–62·4) × 5–7 μ, with an acute apex, and thin or



Text-figs. 15–25. Text-fig. 15. *Heteroporus biennis*: gloeocystidia. Text-fig. 16. *Phellinus ferreus*: (*a*) setae; (*b*) spores. Text-fig. 17. *Sparassis simplex*: spores (from the type). Text-fig. 18. *Clavaria lithocras*: spores (from the type). Text-fig. 19. *Mycoleptodon microcystidius*: spores. Text-fig. 20. *Poria ambigua*: cystidia. Text-fig. 21. *Trametes serpens* subsp. *albida*: (*a*) basidia; (*b*) spores (both from the Taunton collection); (*c*) spores (from the Burnham Beeches collection). Text-fig. 22. *Cyphella ochroleuca*: (*a*) hairs; (*b*) spores (from the type). Text-fig. 23. *Phaeocyphella fraxinicola*: spores (from the Pickering collection). Text-fig. 24. *Poria ambigua*: spores. Text-fig. 25. *Stereum abietinum*: (*a*) cystidia (from the British collection); (*b*) spores (from Norwegian material). All ×866.

thickened brown walls. Setae with strongly thickened walls vastly predominate but, as with many species of *Phellinus*, there are all gradations between the thin-walled hyaline and thick-walled brown states. *Hyphal structure* dimitic, consisting of thick-walled, brown skeletal hyphae, 2–3 μ in diam., with a distinct lumen and very scanty septa, and thin-walled, hyaline, septate, branched, generative hyphae, 1·5–3 μ in diam., lacking clamp connexions. Individual generative hyphae may develop slightly thickened brownish walls, and occasionally the skeletal hyphae may produce a branch.

Habitat on (?) *Quercus* sp., Taunton, Som., coll. A. J. Dodd, 20 Aug. 1955; on dead branch of *Q. ilex*, which was still attached to the tree, in woods above Bossington, near Porlock, Som., coll. D. A. Reid, 23 May 1957 [B.M.S. Spring Foray]; on *Quercus* sp., in woods near Tarr Steps, Dulverton, Som., coll. P. K. Austwick, 24 May 1957 [B.M.S. Spring Foray]; on living branch of a deciduous oak, Upper Horner Valley, near Porlock, Som., coll. D. A. Reid, 28 May 1957 [B.M.S. Spring Foray].

The specimens cited above are the first British collections of *P. ferreus*. However, as three collections were obtained on various species of oak during the Spring Foray of the British Mycological Society at Porlock in 1957, it would seem that the species may be relatively common in the south-western part of the country.

PORIA AMBIGUA Bres., in *Atti Accad. Agiati III*. **3**, 84, 1897 (Text-figs. 20, 24).

Synonyms: *P. consobrinoides* Pilát, in *Bull. Soc. mycol. Fr.* **51**, 380, 1955.
P. reticulato-marginata Pilát, in *Bull. Soc. mycol. Fr.* **51**, 380, 1955.
P. lacerata Murr., in *Mycologia*, **12**, 91, 1920 [teste Bresadola, *Sel. Myc.* **2**, 30, 1926].

Fructification resupinate, forming extensive, white, poroid patches, showing greyish or brownish discoloration especially towards the broad (up to 5 mm.), sterile, determinate, villose margin, which may or may not be fibrillose. *Pores* 0·4–2·0 mm. in diam., varying from round to angular, but frequently torn and irpicoid when the fruit-body is growing in a vertical position. *Spores* hyaline, thin-walled, elliptical, 4·5–6·5 × 3–3·5 μ. *Basidia* clavate, 15–20 × 4–6 μ with four narrow sterigmata. Pilát (1941) and Bourdot & Galzin (1928) state that the basidia may be two- or four-spored. *Cystidia* present, strongly resembling the basidia in size, but having thicker walls and an obtuse or more or less pointed apex, which is usually capped by a crystalline material. Pilát (1941) described the organs as 'ordinairement presέntes, peu différentes des basides dans la forme et dans la grandeur, claviformes souvent rétrécies à la fin et portant un petit capuchon d'incrustation cristalline, 15–25(–30) × 4–5·5 μ (rarement plus grandes). Quelquefois, elles sont dépourvues d'incrustations terminales, et passent ainsi inaperçues.' *Hyphal structure*, monomitic, consisting of freely branched, hyaline, septate generative hyphae, 2–6 μ in diam., with thin but distinct walls, and lacking clamp connexions.

Habitat on beech, Norbury Park, Leatherhead, Surrey, coll. Miss W. Parker, Dec. 1955.

TRAMETES SERPENS (Fr.) Fr. subsp. ALBIDA (Fr.) Bourd. & Galz., in *Bull. Soc. mycol. Fr.* **41**, 167, 1925 (Text-fig. 21).

Fruit-body either entirely resupinate, or becoming effuso-reflexed, with small narrow pilei up to 1 cm. in width, or forming dense clusters of very small imbricate pilei up to 1·5 cm. long and 1·0 cm. wide. When present the pileus is at first covered by a minute pubescence which becomes matted together to form a more or less glabrous, often uneven surface, which varies from 'Cartridge-Buff' to 'Pallid Mouse Gray' or 'Pale Mouse Gray' in the older portions, and may be obscurely zoned with 'Ochraceous-Buff'. The pores are variable in appearance depending upon the position in which the fructification grew. Normally in a horizontal reflexed pileus they are irregularly angular or subdaedaleoid, 0·5–2 mm. in diam., but when borne on a vertical or oblique surface the tubes open and appear almost irpicoid. In the case of pilei forming nodulose clusters, the tubes in a vertical position may form long irpicoid or lamelloid plates up to 1 cm. or more in length. The poroid surface varies in colour from 'Cartridge-Buff' to 'Cream-Buff' but on old resupinate areas may be 'Pallid Mouse Gray'. In resupinate gatherings there is only a very narrow, sterile, determinate margin. *Spores* hyaline, elliptical, with a lateral apiculus, (8–)9–12 × 4–4·5(–5) μ. *Basidia* hyaline, clavate, up to 54·6 μ in length and 6·5–10 μ in width, with a basal clamp connexion, and bearing four straight sterigmata up to 10 μ long and 2 μ wide at the base. *Hyphal structure* dimitic consisting of hyaline, thick-walled, unbranched, skeletal hyphae, 3–4·5 μ in diam., tapering to 2 μ at the thin-walled obtuse apex, and thin-walled, septate, branched generative hyphae, 2–4 μ in diam., bearing conspicuous clamp connexions. Some of the generative hyphae may become rather thick-walled.

Habitat Taunton, Som., coll. A. J. Dodd, 2 Sept. 1956; on dead 'trunk' of *Rosa* sp., Chicksands Wood, Beds, coll. D. A. Reid, 7 Sept. 1956; on branch of beech, Burnham Beeches, Bucks, coll. D. A. Reid, 21 Sept. 1956.

Although *T. serpens* has long been known as a British species, there is no mention in the literature of a pileate state, and no previous record of subsp. *albida* from this country.

HYDNACEAE

MYCOLEPTODON MICROCYSTIDIUS Christiansen, in *Friesia*, **4**, 329, 1953 (Text-fig. 19).

Fructifications forming resupinate, adnate patches, densely covered by slender brownish needles, up to 2·2 mm. in length, and 0·1–0·2 mm. in width, with a paler acute, often penicillate apex. Occasionally adjacent needles may fuse. Under a dissecting microscope the needles of dried specimens appear horny-cartilaginous, and very minutely pubescent. *Spores* hyaline, elliptical, slightly depressed laterally, 3·5–4·5 × 1·5–2 μ. *Basidia* hyaline, clavate, 9–18 × 3–4 μ, with four sterigmata. *Cystidia* very scanty, resembling ordinary hyphal endings, but slightly thicker walled and encrusted apically with mineral matter. These bodies project slightly beyond the basidia, and are best seen in fresh material. *Hyphal structure* monomitic, consisting of generative hyphae, 2–3 μ in diam., with clamp connexions at the septa, and thin but distinct walls.

Habitat on rotten beech stump, Burnham Beeches, Bucks, coll. D. A. Reid, 14 Oct. 1956.

The author wishes to thank Dr M. P. Christiansen for confirming his determination of this species, which is new to the British Isles.

CLAVARIACEAE

Clavaria lithocras Reid, sp.nov. (Text-fig. 18).

Sporophora 6–15 mm. alta, clavata, plerumque simplicia, longitudinaliter sulcata, cremeo-ochracea, apice ipso gutta-'resinacea' aurantiaca capitata; stipes glaber, 3–6 mm. longus, 0·3–1·0 mm. latus. *Sporae* hyalinae, laeves, ellipticae, non-amyloideae, 4–6 × 2·5–3·5 μ. *Basidia* cylindrica, hyalina, quadrispora 16 × 5 μ. *Sterigmata* usque ad 4 μ longa. *Hyphae* hyalinae, inflatae, septatae, sine fibulis, 2·5–15 μ diametro, tenuiter tunicatae.

Sporophore 6–15 mm. high, clavate, normally simple, longitudinally sulcate, appearing angular in transverse section, creamy ochraceous, and capped by a small, hard, orange resin-like exudate. Occasionally a fruit-body, probably as a result of injury, may develop up to three small lateral branches or the apex may become fan-shaped. The fructification consists of a stipe 3–6 mm. long and 0·3–1·0 mm. wide which expands gradually into the fertile club which is 0·8–2·5 mm. wide at the apex. *Spores* hyaline, smooth, elliptical, non-amyloid, 4–6 × 2·5–3·5 μ. *Basidia* cylindrical, hyaline, 16 × 5 μ wide, with four sterigmata up to 4 μ in length. *Hyphal structure* monomitic, consisting of thin-walled, inflating, branched generative hyphae, 2·5–15 μ wide, with abundant septa but lacking clamp connexions. The conspicuous resinous exudate which forms the apex of each club is devoid of hyphae.

Habitat. Very abundant amongst mosses on the peaty bank of a dike, Hod Fen, Yaxley, Hunts, coll. J. Gilbert, 31 July 1956; 13 Aug. 1956 [TYPUS].

This species is well characterized by the small spores, and by the fruit-bodies being capped by a hard, orange, resin-like exudate.

The author wishes to thank Dr E. J. H. Corner for examining specimens of the above collection, and for stating that, so far as he was aware, they belonged to an undescribed species.

THELEPHORACEAE

CYPHELLA OCHROLEUCA Berk. & Br., in *Ann. Mag. nat. Hist.* Ser. 2, **13**, 405, 1854 (Text-fig. 22).

Synonyms: *Phaeocyphella ochroleuca* (Berk. & Br.) Rea, in *British Basidiomycetae*, p. 704, 1922.
Cyphella rubi Fuckel, in *Symb. Mycol.* p. 26, 1870.
Cyphella lactea Bres. var. *rubi* (Fuckel) Pilát, in *Ann. mycol., Berl.*, **23**, 149, 1925.
Cyphella lactea Bres., in *Fung. Trid.* **1**, 61, 1884.

In the previous paper of this series (Reid, 1955) a description was given of *Cyphella lactea* Bres., but it has since been found that *C. ochroleuca* Berk. & Br. is an older, and therefore the correct, name for this fungus.

Massee (1892) stated, quite erroneously, that the spores of *C. ochroleuca* were 'very pale ochraceous, elliptical, 6 × 4 μ', and this led Rea (1922) to transfer the species to the genus *Phaeocyphella*. The fruit-bodies of the type collection 'on bramble, near Batheaston, Oct. 1851, No. 179', bear narrow, elongated, elliptical, hyaline spores (8–)10–12 × 3–4·5 μ with curved bases, and also show the characteristic clavate or capitate hairs on the exterior surfaces.

Pilát (1925) complicated the nomenclature of this species by making *C. rubi* Fuckel a variety of the more recently described *C. lactea* Bres. when he should have made *C. lactea* a variety of *C. rubi*. If Pilát's view is accepted that the fungus on hosts other than *Rubus* is worthy of varietal status, then *C. lactea* should be made a variety of *C. ochroleuca*. However, the author regards the fungus on *Rubus* and other hosts as belonging to a single taxon.

PHAEOCYPHELLA FRAXINICOLA (Berk. & Br.) Rea, in *British Basidiomycetae*, p. 704, 1922 (Text-fig. 23).

Synonym: *Cyphella fraxinicola* Berk. & Br., in *Ann. Mag. nat. Hist.*, Ser. 4, **15**, 32, 1875.

Fructifications consisting of small, sessile, white, villose, concave discs, 200–350 μ in diam., with yellowish cream coloured hymenia and somewhat enrolled margins. *Spores* brown, broadly elliptical, rather thick-walled, 7–8 × 4·5–5 μ. *Basidia* hyaline, clavate 20–26 × 7–8 μ with 4 narrow, curved sterigmata up to 5 μ in length, and a basal clamp connexion. *Hyphal structure* monomitic. The trama is formed of branched, septate, generative hyphae, 2·5–3 μ in diam., bearing clamp connexions, and having thin but distinct hyaline or pale brown walls. Toward the outermost regions of the disc the hyphae diverge to form the villose exterior. These hyphae are covered by a very fine encrusting granular material, and often branch from clamp connexions. A non-thickening hymenium lines the interior of the disc and consists of a layer of basidia 20–26 μ in width. The total thickness of the fruit-body at its widest portion is only 78 μ.

Habitat forming scattered colonies on the bark of *Fraxinus*, apparently associated with an erumpent pyrenomycete, Cluntshell Wood, Pickering, Yorks, coll. W. G. Bramley [K/56/54], 16 Dec. 1956.

The above material, which could easily be mistaken for a minute discomycete, has been compared with the type of *P. fraxinicola*, preserved in the Kew Herbarium. This also appears to be associated with an erumpent pyrenomycete, and has almost identical microstructure and brown elliptical spores 6·5–8 × 4·5–6 μ.

Dr M. A. Donk has drawn my attention to the fact that *Cyphella epissphaeria* Quél. may be synonymous with *P. fraxinicola* and that Rea's (1927) record of this species may represent a further British collection of *P. fraxinicola*. However, Rea gave the spore size of his gathering as 8–9 × 5–5·5 μ.

Sparassis simplex Reid, sp.nov. (Pl. 24, fig. 1; Text-fig. 17).

Sporophorum usque ad 8 cm. altum, 9 cm. latum, stipitatum, flabellatum, in lobis divisum et redivisum, ochraceo-cremeum, marginem versus cremeo-pallescens, obscuraliter zonatum, e strato basali, fertile, corticioideo oriundum. *Stipes* usque ad 2·5 cm.

longus, 0·8 cm. latus, compressus, fertilis. *Hymenium* utrinque productum. *Sporae* subhyalinae, laeves, ellipticae, tenuiter tunicatae, non-amyloideae, 5–9 × 3·5–5 μ. *Basidia* 31·2–46·8 × 4·5–5 μ, clavata, quadrispora, fibulis ornata. *Hyphae tramales* 3·0–13 μ diametro, hyalinae, ramosae, septatae, sine fibulis, crassiter tunicatae. *Hyphae subhymeniales* 2·5–5 μ diametro, sine fibulis, tenuiter tunicatae.

Fruit-bodies up to 8 cm. high, 9 cm. wide, stipitate, flabellate, divided and redivided into numerous flattened lobes, orchraceous-cream, becoming cream-coloured towards the margin, indistinctly zoned, and arising from fertile, concolorous, resupinate corticoid areas, with a white byssoid margin. *Stipe* up to 2·5 cm. long, 0·8 cm. wide, flattened, and covered by the amphigenous hymenium. *Spores* subhyaline, smooth, elliptical, thin-walled, non-amyloid, 5–9 × 3·5–5 μ, but pale ochraceous-cream in the mass. *Basidia* 31·2–46·8 × 4·5–5 μ, clavate, 4-spored, with a basal clamp connexion. The clamp connexions are often difficult to detect and sometimes abnormal. *Hyphal structure* monomitic. *Tramal hyphae* 3·0–13 μ in diameter, hyaline, very much branched, rather loosely arranged, septate, without clamp connexions, and nearly all becoming conspicuously thick-walled, although there are some broad thin-walled conducting hyphae present which stain deeply in aniline blue in lactic acid. The thick-walled hyphae are highly refractive and usually swollen at the septa, where the lumena are likewise enlarged. *Subhymenial hyphae* 2·5–5 μ in diameter, densely compacted, branched, septate, thin-walled, lacking clamp connexions, and forming a zone 30 μ wide.

Habitat growing over coniferous debris (*Pinus* sp.) amongst *Calluna*, Box Hill, Surrey, coll. P. K. C. Austwick, 2 Oct. 1955 [Typus].

This species, with one or more discrete lobed fruit-bodies arising from a fertile resupinate corticioid patch, appears very different at first sight from all other species of *Sparassis*, and suggests a fleshy stipitate member of the genus *Stereum*. However, although there is no attempt at the formation of the characteristic cauliflower-like fructification with a rooting base, the microscopic structure, which is very similar to that of *S. crispa* and *S. laminosa*, together with the presence of an amphigenous hymenium, places it beyond doubt in the genus *Sparassis*.

Collections of *S. crispa* and *S. laminosa* show considerable variation in microstructure. In some gatherings the tramal hyphae are almost all thin-walled, whilst in others many become thick-walled and highly refractive. The distribution of clamp connexions is equally variable; in some specimens clamp connexions are conspicuous and present at almost all the septa, but in others they appear to be completely absent from the tramal hyphae, or very scarce. These differences do not seem to be correlated in any way. In *S. simplex* all the tramal hyphae, at least in the older portions of the fruit-body, become very thick-walled and appear to be much more freely branched than those of *S. laminosa* and *S. crispa*, and clamp connexions are confined to the base of the basidia. The spores of *S. crispa* and *S. laminosa* are indistinguishable, judging from the Kew material, and vary only slightly in the different gatherings. They are subhyaline, thin-walled, broadly elliptical to ovate, 4·5–6·5(–7) × 3–4·5 μ. On some specimens there is a greater proportion of ovate spores produced than on others, but normally broadly elliptical spores predominate. The spores of *S. simplex* are similar to those of the other two species but somewhat larger, 5–8(–9) × 3·5–5 μ, and vary from broadly elliptical to elliptical, with a large proportion of the latter shape.

Like *S. crispa* the present species grows under conifers, whilst *S. laminosa* is said to occur in oak woods. However, there is a specimen of the latter in the Kew Herbarium [Haslemere Foray, coll. R. W. G. Dennis, Sept. 1945] which was collected at the base of a pine tree, so there is no clearly defined difference in habitat.

From the above discussion it would seem that *S. laminosa* is no more than a variety of *S. crispa* with a lax growth form. [The combination *S. crispa* var. *laminosa* was made by Quélet in *Enchiridion Fungorum*, p. 202, 1886], and that *S. simplex* differs sufficiently from *S. crispa* to be regarded as a distinct species.

STEREUM ABIETINUM Pers. ex Fr., in *Epicrisis*, p. 553, 1838 (Text-fig. 25).

Fructification forming large, uneven, irregular, thick, felty, separable pruinose patches, varying in colour from dark 'Vandyke Brown' or 'Bay' in older portions through 'Hair Brown' to 'Light Drab' or from 'Pale Vinaceous Drab' to 'Dark Vinaceous Drab'; margin thick, very dark brown. Sometimes this fungus may be effuso-reflexed, in which case the minutely tomentose upper surface is dark 'Vandyke Brown' or according to Bourdot & Galzin (1928) 'brun marron, sillonés avec zones noirâtres'. *Spores* not seen in the British material, but Bourdot & Galzin (1927) describe them as 'hyalines, oblongues, un peu déprimées latéralement et obliquement atténuées à la base, 9–12 × 4·25–5 μ'. *Basidia* not seen, but Lentz (1955) states that they are '4-sterigmate, with a basal clamp connexion, 72–100 × 6–7 μ'. *Cystidia* subcylindrical, very thick-walled, pseudoseptate, originating at various levels in the thickening hymenium from thin-walled generative hyphae to which they are joined by a clamp connexion. These organs, 5–13 μ in width, may eventually become completely buried or they may project up to 91 μ above the current basidial layer. Those that are buried in the lower regions of the hymenium have conspicuously thickened dark brown walls, but actively growing cystidia have thin-walled hyaline, obtuse or rarely acute apices, often covered with a fine granular deposit soluble in lactic acid. The cystidia are not mere endings of skeletal hyphae curving into the hymenium from the flesh, but they could be regarded as entire, modified, skeletal hyphae of limited growth. *Hyphal structure* rather lax, dimitic, consisting of thick-walled, dark brown, unbranched, pseudoseptate skeletal hyphae, 3–5 μ in diam., and thin-walled, hyaline or pale brown, branched generative hyphae, 2·5–3·5(–4) μ in diam., with clamp connexions at the septa. The skeletal hyphae, which have only a narrow lumen, curve down through the flesh and form a palisade-like zone above the hymenium. The generative hyphae branch freely, often from clamp connexions. The hymenium thickens markedly, reaching 442 μ in width near the margin of the fruit-body, but does not appear distinctly layered in section as the abundant cystidia arise and terminate at different levels. Some of the cystidia may reach 250 μ in length, whilst others arising at roughly the same level may be only 70 μ long.

There is a dense dark-brown zone at the upper surface of the fruit-body (i.e. the surface nearest the substrate in resupinate material) from which thick-walled, dark brown hyphae 2·5–3 μ in diam. grow out to form the tomentum. These hyphae, which branch very rarely, are abundantly pseudoseptate, but may have an occasional clamped septum.

Habitat on imported Yugoslavian whitewood (spruce), which had been in Britain for 3 or 4 years, leg. W. P. K. Findlay, 5 Aug. 1955.

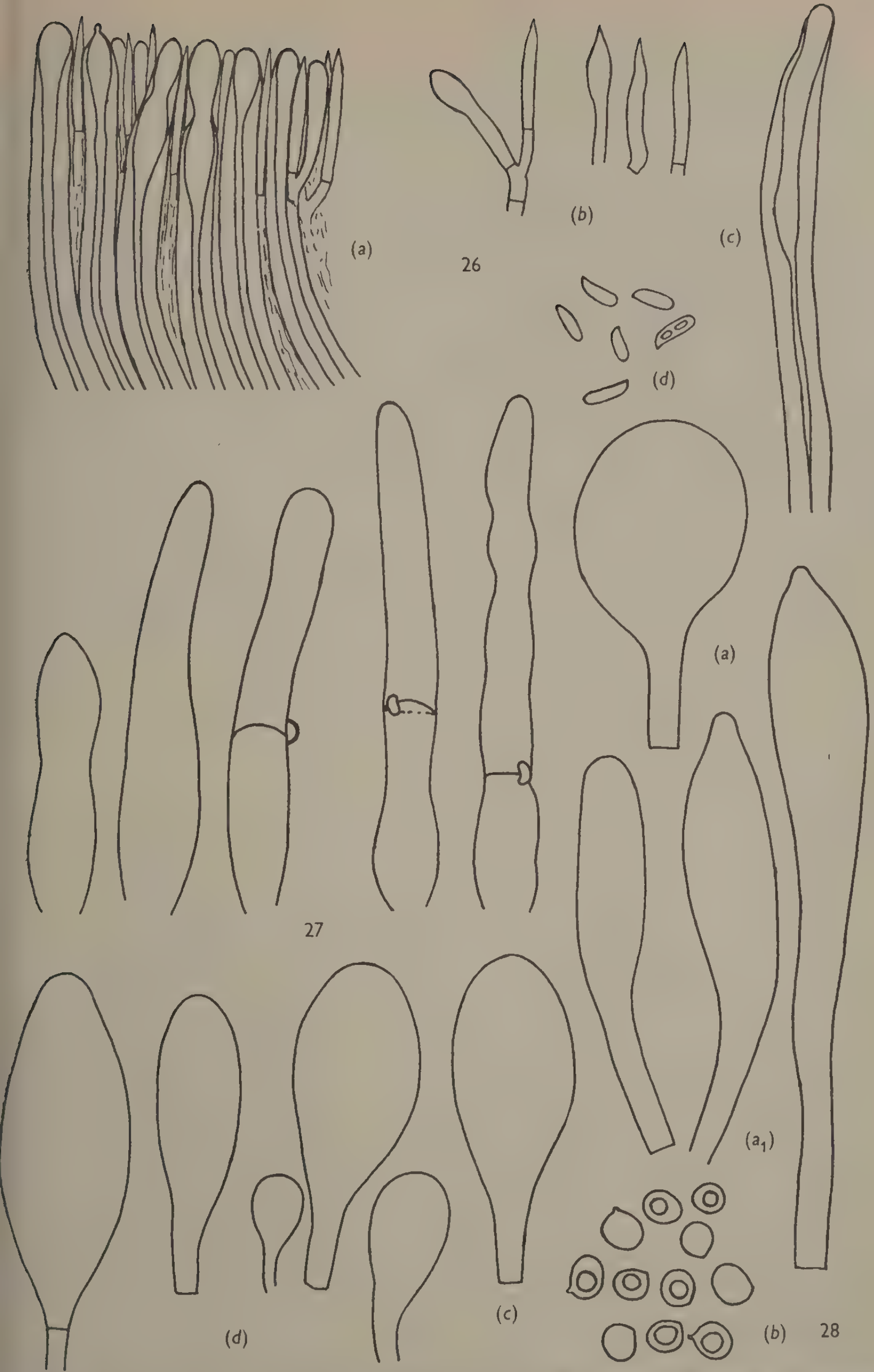
Rea (1922) included *S. abietinum* in his *British Basidiomycetae* and gave its habitat as 'Pine and *Abies* trunks and logs. Rare.' He had apparently never seen British material, so it is probable that it was included on the basis of some obscure record in a county list.

There is a collection in the Kew Herbarium labelled *S. abietinum* by Berkeley, from 'Flintham [?S. Notts.], Sept. 1859'. This gathering was wrongly named, and is *Stereum chailletii* (Pers. ex Fr.) Fr. However, it is conceivable that details of the collection were published and led Rea to include the species as British.

STEREUM SULPHURATUM Berk. & Rav., in *J. Linn. Soc.* (*Bot.*), **10**, 331, 1868 (Text-fig. 26).

Fructifications effuso-reflexed, or forming separable resupinate areas up to 6 cm. or more in length by coalescence of adjacent peltate patches which may at first have conspicuous silvery, fringed, hirsute margins. The upper surface of the pilei, when present, is covered by a thick, shining, whitish or silvery, rather shaggy tomentum, and is often obscurely zoned. The 'Cartridge Buff' or 'Vinaceous Buff' coloured hymenium may be smooth or uneven depending upon the underlying surface of the substrate. *Spores* hyaline, subcylindrical to narrowly elliptical, often somewhat laterally depressed, amyloid, 6–8·5 × 2–2·5 μ. [When examined in Melzer's solution spores up to 10 μ in length were seen.] *Basidia* hyaline, clavate, 19–26 × 4–5 μ, with four curved sterigmata up to 5 μ in length. *Basidioles* abundant, hyaline, fusiform or lanceolate, 20–33·8 × 2–3·5 μ. *Conducting elements* very abundant. These structures, 5–13 μ in diam., are the modified endings of hyaline thick-walled skeletal hyphae, which curve down through the trama into the hymenium, where they are often inflated, but narrow towards the apex which is usually thin-walled, frequently constricted, and sometimes prolonged into a finger-like process. The conducting organs rarely protrude beyond the surface of the hymenium. *Hyphal structure* dimitic, consisting of thick-walled, unbranched, septate, highly refractive skeletal hyphae, 4·5–6 μ in diam., with a distinct lumen, which curve down through the flesh and terminate in the hymenium as somewhat inflated conducting organs, and branched, septate, generative hyphae, 2·4–5 μ in diam. with thin or slightly thickened walls, and lacking clamp connexions.

Habitat. Worcester Foray, Sept. 1921 [determined as pale form of *S. hirsutum*]: Kinloch, Isle of Rhum, Scotland, coll. R. W. G. Dennis, 25 July 1951; on small twigs, Chicksands Wood, Beds, coll. D. A. Reid, 7 Oct. 1956; on twigs of *Fagus sylvatica*, Friston Forest, Sussex, coll. P. D. Orton and P. K. C. Austwick, 17 Nov. 1956; on small branches, King's Langley, Herts, coll. D. A. and P. M. Reid, 1956.



Text-figs. 26–28. Text-fig. 26. *Stereum sulphuratum*: (*a*) section through the hymenium showing conducting elements, basidioles and basidia; (*b*) basidioles; (*c*) conducting element; (*d*) spores (all from Chicksands collection). Text-fig. 27. *Fayodia bisphaerigera*: cheilocystidia (from the Inverness-shire collection). Text-fig. 28. *Pluteus minutissimus*: (*a*) and (a_1) hairs from the stipe; (*b*) spores; (*c*) pleurocystidium; (*d*) cheilocystidia (all from the Bletchley collection). All ×866.

The following collections have also been provisionally referred to thi species: Gopsall, Leics., coll. Rev. A. Bloxam [ex-Herb. Berkeley a *S. hirsutum*]; Kew Gardens, 1884 [ex-Herb. M. C. Cooke as *S. ochroleucum* Fr.].

This species, which had previously been collected in Europe from Germany, France and Czechoslovakia, is very closely related to *S. hirsutum* but can easily be distinguished in the field by the silvery, hirsute pileus and pale 'Cartridge Buff' hymenium. The microscopic structure of both species is very similar, but there is no golden cuticular zone beneath the tomentum in *S. sulphuratum*. It was at first thought that the amyloid reaction of the spores of *S. sulphuratum* would clearly separate it from *S. hirsutum*, but examination of the spores of the latter species showed that when mounted in Melzer's solution and then transferred to water they too gave an amyloid reaction, as stated by Boidin (1950).

S. sulphuratum is probably not uncommon in Britain, and has no doubt been confused with *S. hirsutum*, both in this country and on the Continent. Pilát (1930) stated that in Czechoslovakia it occurs chiefly on the thinner branches of *Rosa*, *Prunus spinosa*, *Betula*, *Populus tremula*, *Quercus*, *Ulmus* and *Fagus*.

Lentz (1955) has given an account of a very similar fungus under the name *S. ochraceo-flavum* (Schw.) Ellis, and his figure (pl. 6B) is very like the British collections described above. However, this species would seem to differ from *S. sulphuratum* in having a bright yellowish hymenium, a yellowish brown cuticular layer, and also in lacking basidioles.

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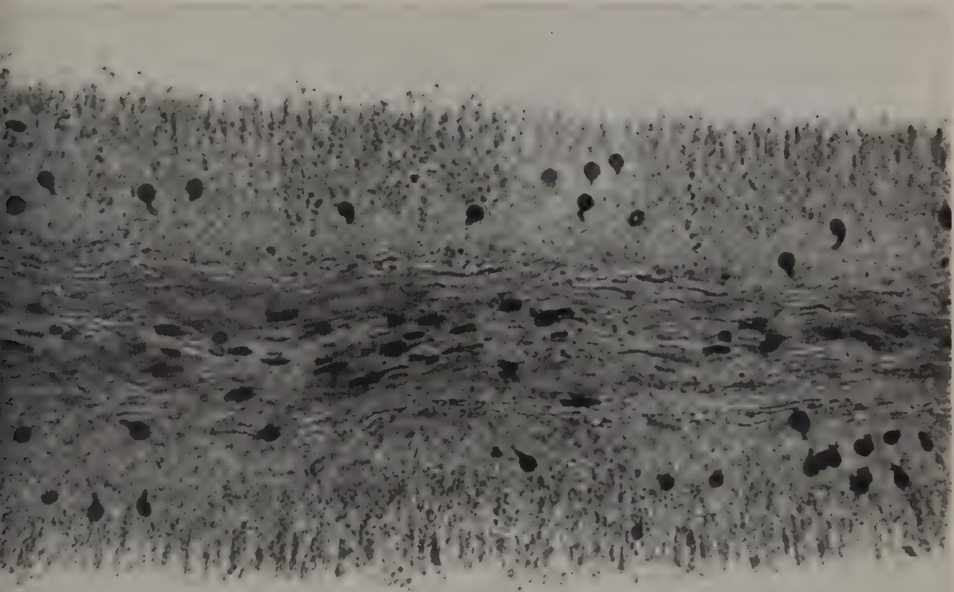

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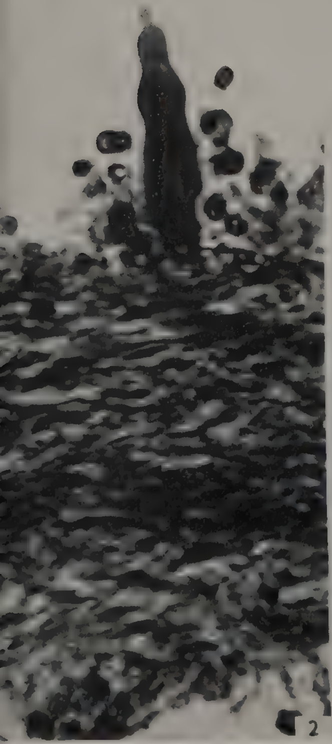

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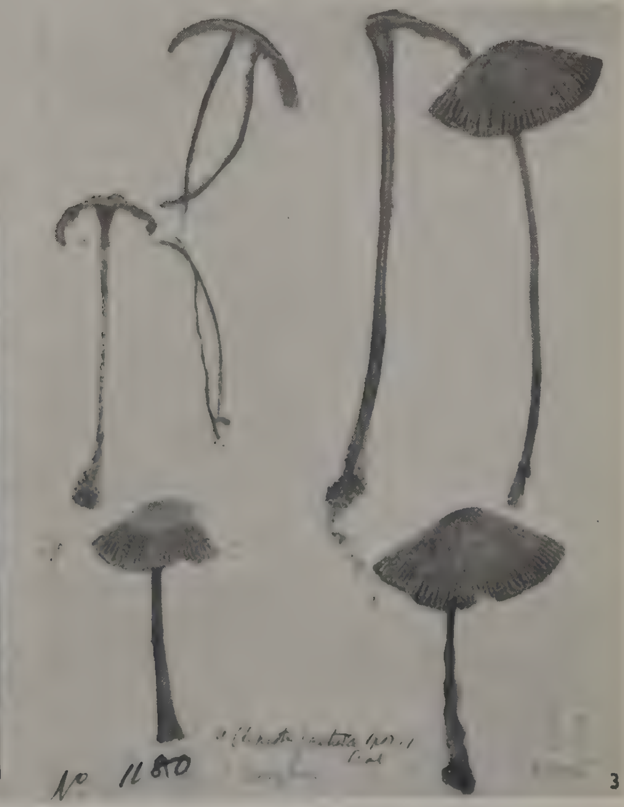

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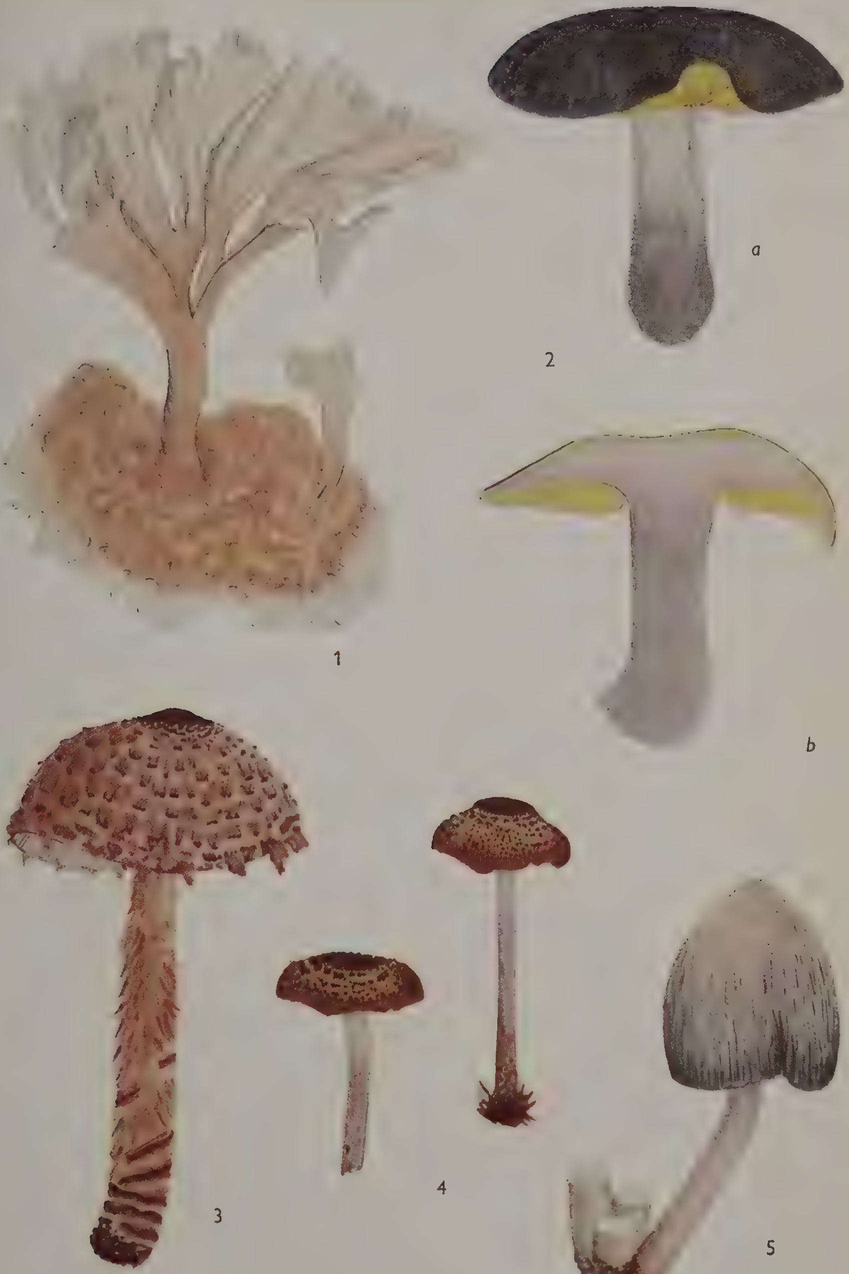
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EXPLANATION OF PLATES 23 AND 24

PLATE 23

Fig. 1. *Lentinellus cochleatus*: part of a vertical section through a gill showing chlamydospores in the subhymenia. × 350.

Fig. 2. *Heteroporus biennis*: part of a vertical section of the pore wall showing a gloeocystidium. × 350.

Fig. 3. *Lepiota metulaespora*: photograph of the type collection. × 1.

PLATE 24

Fig. 1. *Sparassis simplex*: part of the type collection. × two-thirds.

Fig. 2. *Lyophyllum favrei*: (*a*) complete sporophore; (*b*) longitudinal section. × two-thirds.

Fig. 3. *Lepiota ventriosospora*: type specimen. × two thirds.

Fig. 4. *Lepiota eriophora*: Bridgwater collection. × two-thirds.

Fig. 5. *Coprinus insignis*: × two-thirds.

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HELICOMA MONOSPORA SP.NOV. FROM PINE LITTER

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(With Plate 25)

The morphological and ecological characteristics of *Helicoma monospora* sp.nov., which is of frequent occurrence on decaying leaves of *Pinus sylvestris*, are described.

Helicoma monospora sp.nov. (Plate 25)

Coloniae sparsae. *Hyphae* fuscae, septatae, prostratae, anastomosantes, reticulum sparsum in utraque pagina foliorum formantes. *Conidiophora* 11–38 × 2·5–3·5 μ, sparsa, pallide fusca, simplicia, erecta, septata. *Conidia* solitaria, acrogena, sessilia, nigra, 4–5-septata, in septis non constricta, septis atris, filamentis 6–9 μ crassis, convolutis semi-helicem 8·5–13 μ diametro formantibus, cellulis basalibus atque terminalibus subhyalinis. *Hab.* in foliis putridis Pini sylvestris L. Delamere, Cheshire, Anglia. *Holotypus* Herb. I.M.I. No. 71429. Species haec ex affinitate *H. isiola* Moore, sed conidiis solitariis acrogenis, 4–5-septatis, 8·5–13 μ diametro, semper ex conidiophoris solitariis, erectis, septatis, egredientibus, dignoscitur.

Hyphae darkly pigmented, septate, forming a fine, anastomosing, surface reticulum. *Conidiophores* 11–38 × 2·5–3·5 μ (11–25 × 3–3·5 μ in culture) light brown, erect, septate, never branched, arising singly at intervals along the repent sterile hyphae, frequently with a slight basal swelling. *Conidia* single, terminal, sessile, non-deciduous, lustrous black, with heavy pigmentation in the cell walls, the terminal cell and basal cell having much less pigment than the others. Septa 4–5, conidial diameter 8·5–13 μ (9–10·5 μ in culture) conidial filament 6–9 μ thick (5·5–6·5 μ in culture). *H. monospora* was first observed in September 1955 on decaying needles of *Pinus sylvestris* from the F 1 layer of the Ao horizon of a podzol at Delamere Forest, Cheshire.

The fungus was obtained in pure culture by picking off conidia from heavily infected needles, and plating them on 2 % malt-extract agar at pH 5. The spores germinate in a few days at room temperature, and the mycelium grows very slowly to form a compact, slightly raised, velvety colony of a most intense black colour. The formation of conidia in culture only occurs after a long period of vegetative growth. Many of the conidia are seen to have germinated or grown on from the terminal cell, while still attached to the conidiophore, producing long, septate, light brown hyphae. Various anomalous conidia have been observed in culture which are not found on the natural substrate. The usual form exhibits a reduced or absent recurvature of the conidium. Conidia with two opposite recurved portions re also occasionally seen. If the fungus is inoculated onto the surface of terile brown needles from the L layer of the Ao horizon, vigorous growth and sporulation occur. When the mycelium is allowed to grow out from a nutritive medium on to a glass surface, the typical reticulum of vegetative hyphae with scattered condiophores develops (Pl. 25, fig. 2).

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Moore (1955) gave a key to thirty-three species of *Helicoma*, and subsequently (Moore, 1957) recognized three further species. Of these thirty-six species, *H. monospora* resembles only *H. isiola* Moore. In *H. isiola* there are no conidiophores, the conidia usually arising directly from the myce-ium, often in glomerulae, or being produced acropleurogenously on short ateral branches, which from Moore's illustration appear aseptate. The conidia of *H. monospora* never arise directly from the mycelium, nor do they form glomerulae, being invariably solitary and acrogenous on scattered, erect, septate conidiophores. The conidia of *H. isiola* are 10–17 μ diam., while those of *H. monospora* are 8·5–13 μ only. Moore does not give a range for the number of septa in the conidium of *H. isiola*, though of the conidia in his illustration, one appears to possess six septa and the other seven. *H. monospora* has four or five.

One of the most interesting features of *H. monospora* is its apparently restricted habitat. Of the four layers into which the Ao horizon at Delamere can be divided, *H. monospora* inhabits only the F 1. Within this layer, however, conidiophores are present on over 90 % of needles observed. Single needles bearing more than 10,000 conidiophores are occasionally observed, while needles with over 1,000 conidiophores are common. The reticula and conidia of this fungus constitute one of the main factors in the darkening of the needles which characterizes the F 1 layer. In autumn, conidium formation declines, but the frequency of occurrence remains high throughout the year. Linder's (1929) observation that the Helicosporae can successfully utilize both pectin and cellulose as their sole carbon source suggests that *H. monospora* may be responsible for the breakdown, first of the middle lamellae of the cells of the epidermis, then of the cell walls. This fungus has been observed on decaying needles of *P. sylvestris* at Oxshott, Surrey, by Dr S. J. Hughes, (Herb, I.M.I. No. 25539*b*), thus it appears probable that it is widely distributed, at least in England, wherever its specialized habitat is to be found. The writer would be grateful for records or specimens from any locality.

The conidia of *H. monospora*, as already noted, are not deciduous, but there is every indication that they are nevertheless dispersed, as examination of layer F 2 needles reveals that some physical agency has removed the proliferous conidia found in layer F 1. Conidia have been observed, apparently unharmed, in the excreta of several species of large litter-inhabiting mites. These droppings are frequently observed on the needles of layer L, and radiating hyphae are often seen to emerge from such excreta on the older needles of layer L. Conidia may also be broken off and carried around on the long bristles of several types of soil microfauna observed. Much of the spread of the fungus within the Ao horizon must, however, be attributed to the growth of vegetative mycelium between needles in contact with each other.

This study was carried out under the supervision of Prof. A. Burge during the tenure of an Agricultural Research Council Research Studentship. The writer wishes to thank Dr D. Parkinson for his encouragement, Dr M. B. Ellis of the Commonwealth Mycological Institute, Kew, for his advice on taxonomic matters, Dr S. J. Hughes of the Canada Department of Agriculture, Ottawa, for permission to quote his collection, and Dr V. H. Heywood for his help with the Latin diagnosis.

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EXPLANATION OF PLATE 25

Fig. 1. Reticulum and conidiophores *Helicoma monospora* sp.nov. on a needle of *P. sylvestris* from layer F 1 of Ao horizon. × 100.

Fig. 2. Reticulum and conidiophores on a glass surface. × 700 (the normally erect conidiophores have been flattened for photographic purposes).

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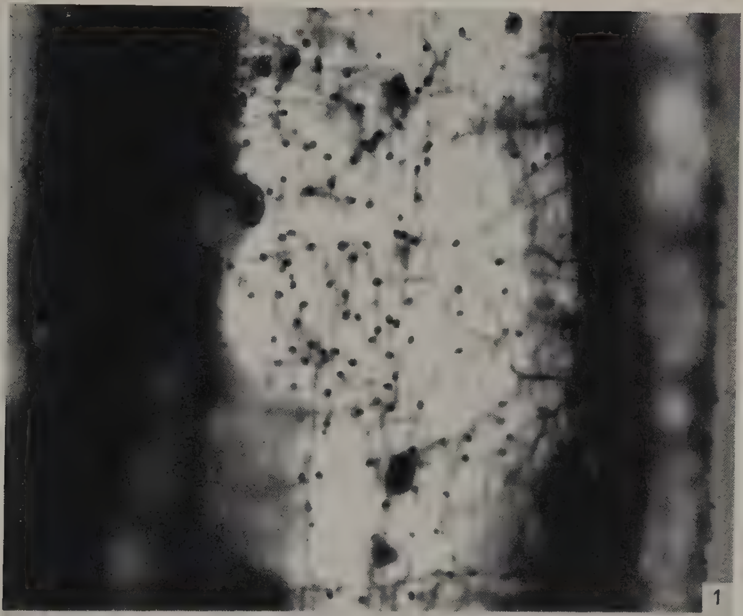

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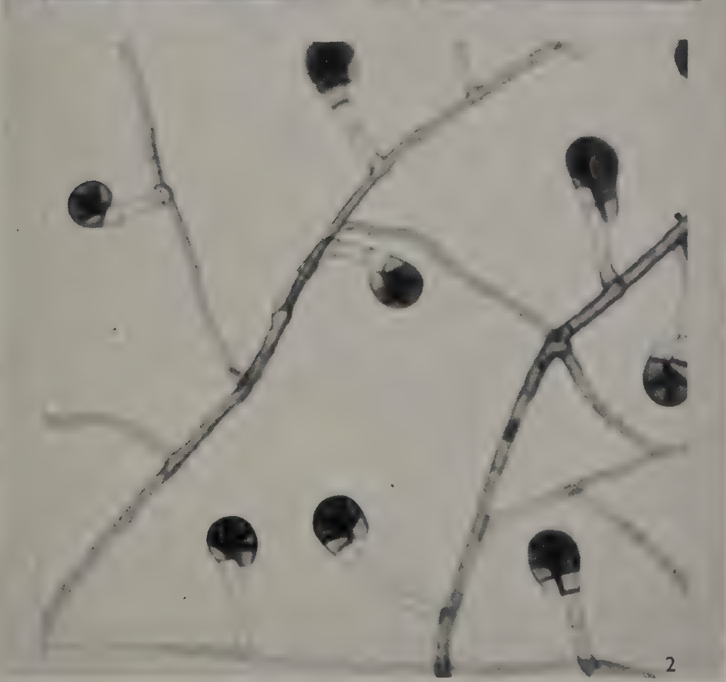

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SPORE DISPERSAL IN *OPHIOBOLUS GRAMINIS* AND OTHER FUNGI OF CEREAL FOOT ROTS

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(With 3 Text-figures)

During Oct. 1953, air was sampled with a Hirst automatic volumetric spore trap at a height of 0·5 m. above the stubble of a wheat crop bearing fructifications of *Ophiobolus graminis*, *Cercosporella herpotrichoides* and *Fusarium culmorum*. Ascospores of *O. graminis* were never caught on rainless days; nor after rain of less than 0·01 in. They were caught within an hour of 0·01 in. or more rain and attained a maximum concentration of 3700 per m.^{3} of air within 2 hr. of 0·05 in. rain. Wind-tunnel tests showed that the peak rate of liberation occurred within 45 min. of wetting. All mature ascospores seemed to be discharged during 4 hr. of rain, but a few dry days sufficed for another batch to mature. *C. herpotrichoides* behaved differently: a few conidia occurred after a trace of rain, and more rain did not increase their numbers; their maximum concentration was only one-tenth of *O. graminis*. Concentrations of coloured basidiospores were more nearly constant, regardless of weather and time of day, and *Cladosporium* was more common by day than by night. No macroconidia of *Fusarium* were detected.

Introduction

In the autumn of 1953 one of the automatic volumetric spore traps devised by Hirst (1952) was used to study the air spora over a field of wheat stubble before ploughing. The primary object was to study spore liberation of *Ophiobolus graminis* Sacc. and *Cercosporella herpotrichoides* Fron. In the following autumn spore liberation from stubble infected by *O. graminis* and *C. herpotrichoides* was tested under partly controlled conditions in a wind tunnel. Filiform ascospores of *O. graminis* are known to be ejected into the air when the perithecia are wetted by rain (Samuel & Garrett, 1933). The filiform conidia of *C. herpotrichoides* are thought to be splashed into the air by the impact of raindrops (Sprague & Fellows, 1934; Oort, 1936; Glynne, 1953). The effect of changes in weather on these two pathogens offered promise of an interesting comparison with saprophytic components of the air spora such as basidiospores and the ubiquitous *Cladosporium*.

The method of operating the trap has been described by Hirst (1952, 1953). The trap was placed so that the orifice was at a height of 18 in. above ground level. Sampling at the rate of 14·4 m.^{3} per 24 hr. was continuous for three periods, 7–14 Oct., 21–23 Oct. and 25 Oct.–1 Nov. The trap was placed in Great Field I, Rothamsted Experimental Farm, in wheat stubble from a crop of cultivar Nord-Desprez which had been harvested in late August. This experimental field had carried four winte wheat crops in the previous 5 years (Salt, 1955) and the incidence o *O. graminis*, *C. herpotrichoides* and *Fusarium culmorum* was high. From 30 t 80 % of the area of plots near the trap were affected by take-all (*O. graminis*) patches at harvest. The site of the trap was approximately 100 m. from a recording rain gauge, from which records were obtained. After exposure, the slides were mounted for examination in 'Solvar'-lacto-phenol mixture (Hirst, 1952) and scanned under the oil-immersion objective. At first spores were counted on cross traverses 4 mm. apart, representing 2-hourly intervals, subsequently intermediate counts were made during periods when *O. graminis* was actively liberating spores.

The efficiency of the Hirst trap is always less than 100 % and varies with wind speed and particle size, so that unless corrected all estimates of spore concentration are low. Efficiency probably averages about 80 %, and to express our results as the number of spores per $m.^3$ of air we have applied an approximate correction as follows: the number of spores counted on each cross traverse, representing the content of one-eighty-third of a cubic metre of air, has been multiplied by 100 instead of 83.

SPORE TRAPPING IN THE FIELD

Data are presented for three fungi inhabiting the wheat stubble and for three important components of the air spora. The total numbers of spores of each type, observed in the preliminary 2-hourly counts (i.e. omitting the additional counts made when *O. graminis* was liberating ascospores) and the maximum concentrations recorded during the survey are shown in Table 1.

Table 1. *Total number of spores and maximum concentration per cu.m. in 2-hourly counts*

Spore type	Total counted in 204 traverses	Max. conc. number per $m.^3$
Important components of the air spora		
Basidiospores (red and brown)	717	1,900
Basidiospores (yellow)	2824	10,000
Cladosporium conidia	1367	139,000
Pathogens on wheat stubble		
Ophiobolus graminis ascospores	190	3,700
Cercosporella herpotrichoides conidia	50	300
Fusarium macroconidia	0	0

Important components of the air spora

Red, brown, and yellow basidiospores were caught at all times. At first, red and brown basidiospores were more numerous, later the yellow basidiospores predominated. Diurnal periodicity (Fig. 1) was almost the reverse of that obtained in summer and early autumn (Hirst, 1953), possibly because lower temperatures were checking spore liberation at night. *Cladosporium*, however, was as reported by Hirst (1953), more common by day than by night.

Pathogens on wheat stubble

In contrast to conidia of *Cladosporium* and basidiospores the occurrence of ascospores of *O. graminis* and conidia of *C. herpotrichoides* was clearly associated with rain.

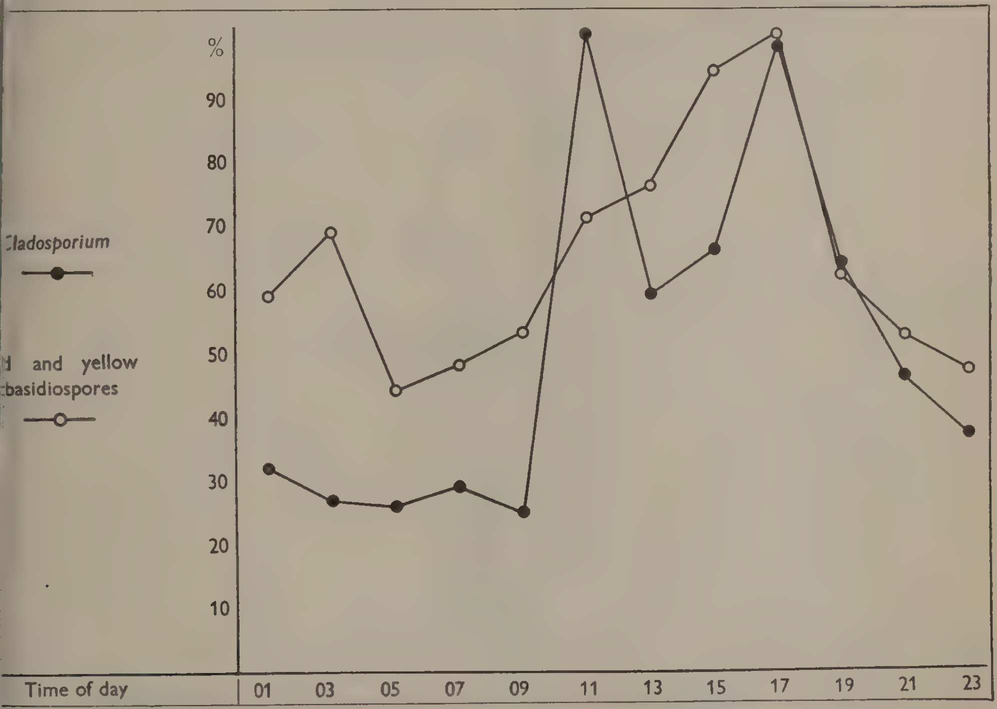

Fig. 1. Mean diurnal periodicity curves of *Cladosporium*, and of red and yellow basidiospores expressed as a percentage of the peak mean concentration.

Ophiobolus graminis

Specimen slides of the ascospores of *O. graminis*, prepared from perithecia on stubble near the trap, confirmed the confidence placed in distinguishing them from other components of the air spora. Ascospores were not caught on the 7 rainless days, and Fig. 2 shows only the 9 days with rain. Ascospores were found only after more than 0·01 in. of rain (Table 2).

Rain on 12 Oct. ended a dry spell which had lasted 20 days. No ascospores were detected when a trace of rain was recorded at 13·00 hr., but after 0·02 in. of rain between 21.00 and 22.00 hr. the concentration rose to 200 per m.^{3} In the next hour 0·08 in. fell and the concentration rose to 3700 per m.^{3}, after which, despite a further 0·02 in., it declined rapidly to zero at 02.00 hr. Further heavier rain between 05.00 and 12.00 hr. on 13 Oct. caused renewed discharge. Maximum concentration, however, reached only 1300 per m.^{3} at 08.30 hr. and later in the same day several traces of rain produced no detectable liberation at all.

The liberation of ascospores during a period of prolonged rain was illustrated on 27 Oct. when 0·6 in. of rain fell between midnight and 15.00 hr. Ascospores were caught at the end of the first hour, a maximum

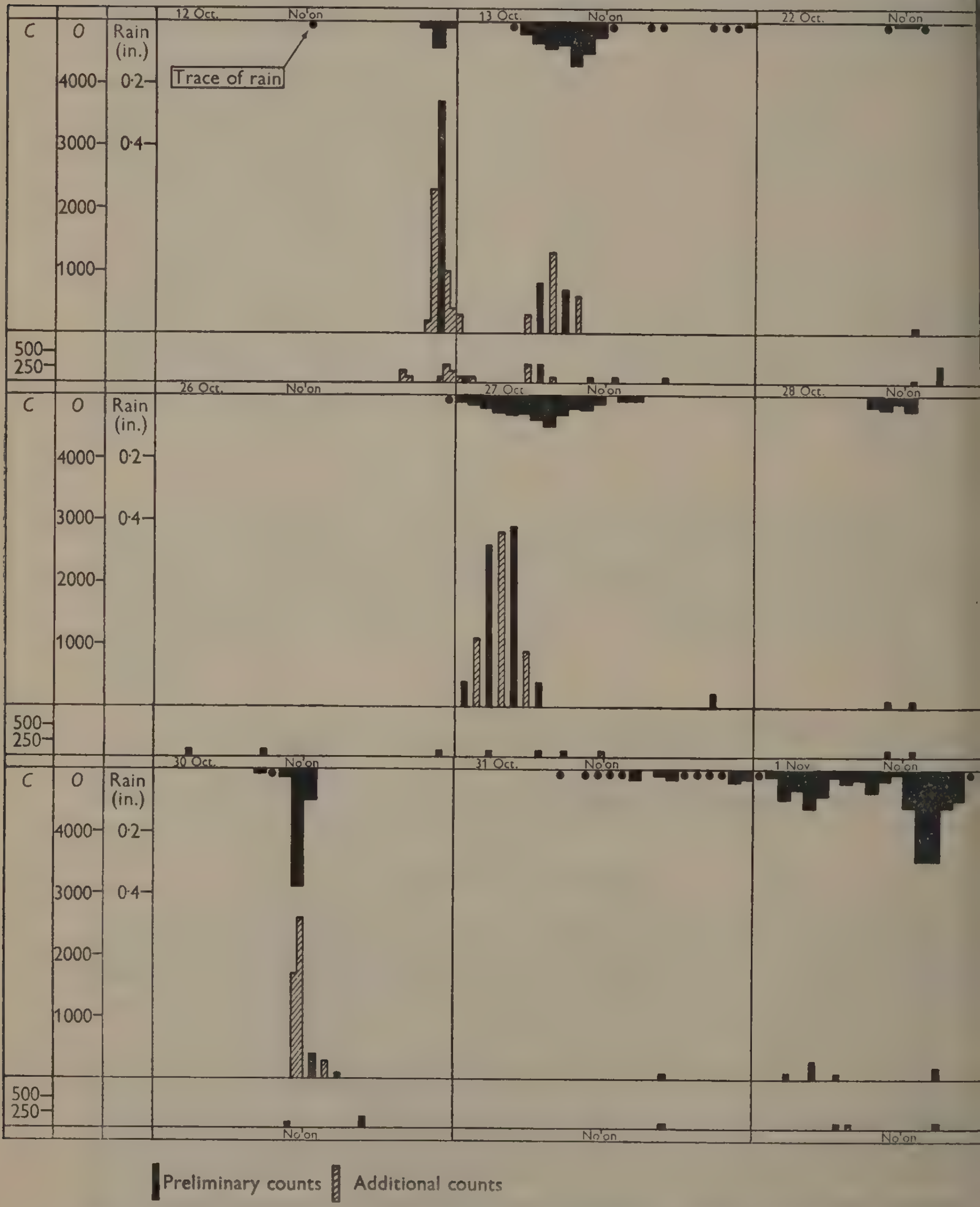

Fig. 2. Number of ascospores of *O. graminis* (*O*) and conidia of *C. herpotrichoides* (*C*), 18 in. above ground-level over wheat stubble, Great Field I, Rothamsted Experimental Farm, in relation to rainfall on 9 days between 12 Oct. and 1 Nov. 1953. (No ascospores were caught on 7 rainless days.)

concentration of 2900 per m.^{3} was reached at 05·00 which declined to zero by 08.00 hr. Despite the occurrence of even heavier rain within the next 6 hr., no more ascospores were detected. The supply of ascospores was renewed by 30 Oct. when the concentration rose to 2600 per m.^{3}, but on 1 Nov. heavy and prolonged rain at a temperature similar to that on 30 Oct., liberated only a few.

Table 2. *Relation between rainfall and ascospore discharge in* Ophiobolus graminis

Rainfall measured in 1 hr. period	No. of periods	No. of occasions when *O. graminis* occurred in next period
Nil	328	0
Trace (<0·01 in.)	24	0
0·01–0·05 in.	31	16
0·05 and over	25	17
Total	408	33

Cercosporella herpotrichoides

This fungus, which causes 'eyespot' of wheat, was abundant on the stubble near the trap, and from these lesions specimen slides of the conidia were prepared. The spores are straight or slightly curved, septate, filiform, and range in length from 30 to 80 μ; the wider end is rounded, the other gradually tapered to a fine point. They cannot be recognized on the trap slides with such certainty as the ascospores of *O. graminis*, and the results must be interpreted as including all spores which fit the above description. Very few were caught and the maximum count for any cross traverse was 3 conidia. Such meagre catches permit only a few tentative conclusions and more extensive tests are needed. The spores were caught only during rainy periods, but unlike *O. graminis* ascospores, as many were caught with light as with heavier rain.

Fusarium

Some fusiform spores were observed on the slides, but few were curved and none had the pedicel characteristic of *Fusarium*. It is thought that these spores were all ascospores and in spite of the proximity of *F. culmorum*, no *Fusarium* macroconidia were recorded in the samples. It is not known to what extent the material was sporulating on the stubble.

WIND-TUNNEL TESTS WITH *OPHIOBOLUS GRAMINIS*

In a further study of ascospore discharge, a small wind tunnel (Gregory, 1951) was used to test the effect of wetting wheat stubble known to be heavily infected with *O. graminis*. The stubble collected in mid-Oct. 1954 was divided into batches of approximately 130 straws. These were spread horizontally on a piece of zinc gauze measuring 11 × 15 in., which was placed midway between the top and bottom of the tunnel and on the same level as a spore trap orifice 6 ft. downwind. For most tests a modified automatic volumetric spore trap was used; when short-period samples were needed a trap was used which had the same orifice dimensions but a static slide (Gregory, 1954). Rain was simulated by wetting the straws from above with a sprinkler; the equal amounts of water given to every batch were sufficient to wet the straws thoroughly, and the excess drained away through the gauze beneath. Air from outside the building was drawn directly through the tunnel at a constant speed of 2 miles per hour. On the moving slide, cross traverses were scanned every millimetre, corresponding to 30 min. intervals. Because of uneven distribution on the static slide, counts were made at millimetre intervals perpendicular to the long axis of the deposit so that the total number of ascospores caught could be reliably estimated. In all experiments the trap orifices were placed centrally in the tunnel facing up-wind. Spore concentrations were not estimated because they would apply only to this one position. Instead, all results are expressed as the number of ascospores deposited per square millimetre of orifice cross-sectional area per hour.

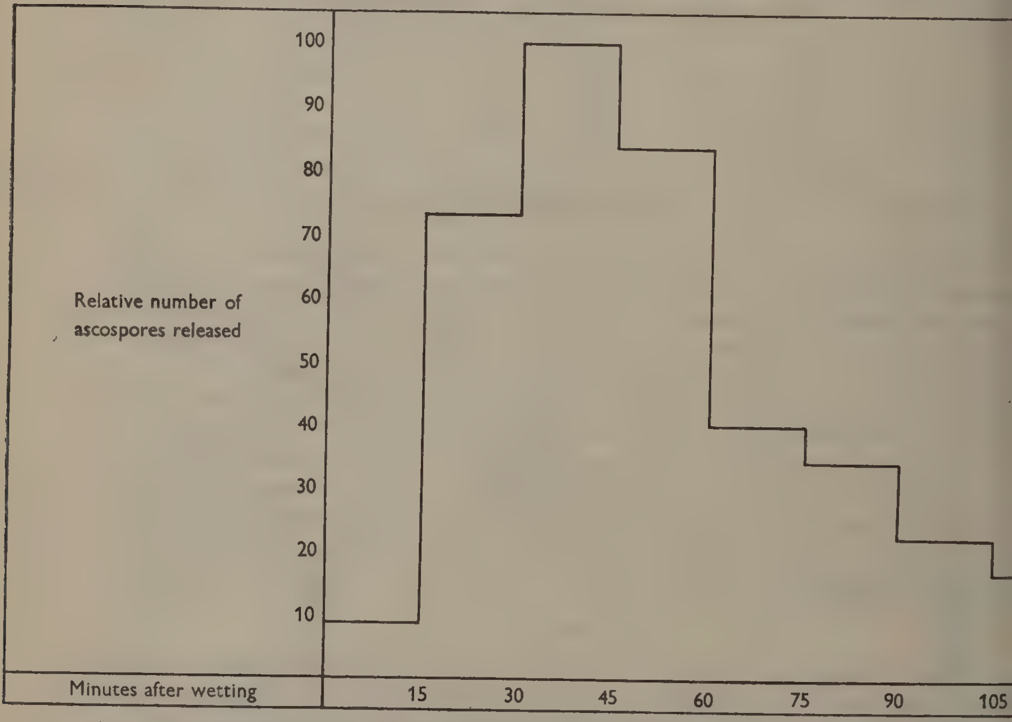

Fig. 3. Relative numbers of *O. graminis* ascospores released at 15 min. intervals after wetting in wind tunnel, expressed as a percentage of the peak numbers liberated.

Several control runs, each lasting 24 hr., were made with dry straws. The first batch was tested the day after collection, other batches were pretreated by being kept moist over damp peat for 48 and 96 hr., but from no batch were any ascospores caught. A further batch was wetted after it had been in the tunnel for 4 hr.; ascospores were first caught in the trap soon after wetting.

To measure accurately the rate of ascospore liberation, the trap with a static slide was used and the slide changed every 15 min. Seven batches were tested in this way. The counts obtained from corresponding intervals after wetting were added together and these totals were expressed as percentages of the maximum (Fig. 3). Liberation started within 15 min., reached its maximum within 45 min. and then declined so that after 2 hr. it was down to 15 % of its peak rate. Counts of automatic trap slides used in other experiments showed that liberation would have continued to decline after this, and after 4 hr. it would have almost ceased. Single ascospores were caught up to 24 hr. after wetting. Seven batches of straws were wetted twice in 24 hr., the second wetting 12 hr. after the first. Irrespective of whether the second wetting was in daylight or darkness, it always gave fewer ascospores than the first. The number of ascospores caught after the second wetting expressed as a percentage of the number caught after the first wetting, shows a range between 3·5 and 47 %; the mean for the seven tests was 21 %.

To find the minimum quantity of water required to start ascospore liberation, a batch of straws was sprayed from an atomiser on 3 consecutive days. On each occasion six pads of absorbent filter papers, which were weighed before and after wetting, were laid at random on the straws. The rainfall equivalent to the increase in weight was then calculated. In the three tests water equivalent to 0·013, 0·007, and 0·021 in. of rain was applied, and, respectively, 17, 0 and 48 ascospores were counted per m.^{2} of orifice cross-sectional area within 2 hr. after wetting. The minimum quantity of rainfall necessary to start release therefore appears to be approximately 0·01 in.

Although the stubble used in wind-tunnel tests was not examined for *C. herpotrichoides*, the fungus was almost certainly present. On none of the slides counted, however, were any conidia detected.

DISCUSSION

The ascospores of *O. graminis* are known to be discharged into the air by active ejection from the ascus (Samuel & Garrett, 1933). Evidently during warm dry weather some asci will mature, to be released as soon as rain has sufficiently wetted the perithecia. Traps in field and wind tunnel both indicate that at least 0·01 in. of rain is needed to start the release mechanism, and in the field 0·08 in. was enough to produce the maximum concentration of 3700 per m.^{3} in less than 2 hr. During prolonged or intermittent rain, the accumulation of mature ascospores was apparently exhausted, an interpretation that was confirmed by results from the wind tunnel. For example, on 13 Oct., heavier rain than had occurred 9 hr. earlier on 12 Oct. failed to reproduce the concentration of 3700 ascospores per m.^{3}, and on 27 Oct. the concentration declined after 5 hr., although rainfall was still increasing. By the end of October the perithecia were probably becoming exhausted, as there was no great difference in temperature to account for the low catches after rain on 1 Nov. The behaviour of *O. graminis* shows a general resemblance to that of *Venturia inaequalis* (Cooke) Wint., reported by Hirst, Storey, Ward & Wilcox (1955), although peak liberation with *O. graminis* occurs within the first hour and with *V. inaequalis* not until the third hour after wetting.

The conidia of *C. herpotrichoides* are thought to be dispersed by rain splash (Sprague & Fellows, 1934; Oort, 1936; Glynne, 1953). The presen meagre data suggest that dispersal is actuated by much less rain than is required by the ascospores of *O. graminis*, that dispersal is not increased by heavy rain and that it continues throughout rainy periods, in contrast to the emission by *O. graminis*.

The failure to catch macroconidia of *Fusarium culmorum*, which are also thought to be dispersed by rain splash, is surprising. There is very little published information about dispersal by rain splash, but it appears a much less efficient method for producing high concentrations of spores in the air than the successful ascus-gun mechanism of *O. graminis*. However, rain splash dispersal may well be an efficient method for scattering spores over an area of a few inches radius around a source. The ability of large spatter droplets to penetrate the slit orifice of the trap is also in doubt.

Mention must be made of the remarkable fact that, in spite of repeated experiments, the ascospores of *O. graminis* have not been shown to infect wheat plants grown in non-sterile sand (Garrett, 1956) and the behaviour of the take-all fungus as a crop pathogen is generally accounted for without the intervention of ascospores. It is, of course, possible that ascospores have lost their original function, perhaps as a result of the change in the status of *Triticum* since man began to cultivate it on a large scale. However, persistence of ability to discharge ascospores may be taken as *a priori* evidence that these spores have some function even if at present it is unknown. The hypothesis that ascospores may be capable of starting infection on some site or host under conditions which remain to be discovered should be experimentally productive and would not conflict with the evidence that ascospores do not play a significant part in the usual epidemic cycle.

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ON THE PLANKTONIC CHYTRIDS *ZYGORHIZIDIUM MELOSIRAE* CANTER AND *Z. PLANKTONICUM* CANTER

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(With 1 Text-figure)

The results of a study on the planktonic parasites of the genus *Zygorhizidium* which infect *Melosira* sp., *Asterionella* sp. and *Synedra* sp. indicate that one taxon, *Z. melosirae* Canter, is involved. Since the binomial *Z. planktonicum* Canter has never been validly published, it is not necessary to reduce it to synonymy.

Two British species of *Zygorhizidium*, *Z. melosirae* Canter (1950) and *Z. planktonicum* Canter, have been described (Canter & Lund, 1953). Because the description of the latter was unaccompanied by a Latin diagnosis the name is illegitimate. Nevertheless, Canter has distinguished between the two primarily on the shape of the resting spore, the size of the male cell, and the occurrence on different hosts. *Z. melosirae* was found by Canter to be parasitic on *Melosira italica* subsp. *Subarctica* O. Müll. and *Z. planktonicum* on *Asterionella formosa* Hass. and *Synedra ascus* var. *angustissima* Grun.

In a previous paper (Paterson, 1956) a parasite of *Synedra* sp., believed to be *Z. planktonicum*, was reported from Douglas Lake, Cheboygan County, Michigan. Indeed, this was the first report of the occurrence of *Z. planktonicum* in the United States. Subsequent to the discovery of the Douglas Lake fungus, abundant material of parasites belonging to the genus *Zygorhizidium* have been found on *Melosira* sp., *Asterionella* sp. and *Synedra* sp. in several Michigan lakes. The following is a tabulated list of occurrences:

Host	Lake	Date
Synedra sp.	Douglas, Cheboygan County	Aug. 1954
Synedra sp.	Portage, Washtenaw County	Feb., March, Apr., 1955
Asterionella sp.	Frains, Washtenaw County	Oct. 1954
Asterionella sp.	Silver, Washtenaw County	Nov. 1954
Melosira sp.	Frains, Washtenaw County	Nov. 1954
Melosira sp.	Base, Washtenaw County	Nov. 1954

Although Canter has described one species of *Zygorhizidium*, *Z. melosirae*, as parasitizing only *Melosira* and the other, *Z. planktonicum*, infecting *Asterionella* and *Synedra*, in the present investigation no morphological difference could be detected between the fungi attacking the various diatoms. Evidence of differences on the basis of size is not conclusive. Table 1 shows all structures described by Canter for *Z. planktonicum* to be consistently smaller than those for *Z. melosirae*. Since, however, the description of *Z. planktonicum* was based entirely on observations on material in formalin, it is conceivable that the structures were smaller because of shrinkage caused by the preservative. Furthermore, Table 1 shows the sizes of such structures as zoospores and sporangia of *Z. planktonicum* to be smaller than those of the Michigan fungus on *Melosira* sp., the *Synedra* and *Asterionella* parasite was similar if not identical in size with Canter's species on *Melosira*.

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* Portion of a thesis accepted in partial fulfilment of the requirements for a degree of Doctor of Philosophy in the University of Michigan.

Table 1. *Data on some of the morphological features found in* Zygorhizidium melosirae *Canter*, Z. planktonicum *Canter, and species of* Zygorhizidium *from several Michigan lakes*

	Species of *Zygorhizidium* found on *Melosira* sp. in Michigan	*Z. melosirae* Canter	Species of *Zygorhizidium* found on *Synedra* sp. and *Asterionella* sp. in Michigan	*Z. planktonicum* Canter
Zoospores diam. (μ)	2·5–3	2·8–3·3	2·5–3	2
Sporangia				
Size (μ)	7–9 × 10·5–13·5	7–14 × 5–10	7·5–12 × 8–13·5	4–9 × 3–8
Shape	Obpyriform	Ovate	Obpyriform	Obpyriform
Resting spores				
Size (μ)	Not observed	9·5–10 × 6–7·5	7·5 × 10	7–8 × 6·5–7·5
Shape	—	Ovate	Spherical—ovate	Subspherical—oval
Male thallus	—	'Unaltered' zoospore	Larger than zoospore cyst	Larger than zoospore cyst
Rhizoids	Branched	Unbranched or sparingly branched	Branched	Richly branched

Additional differences found in the English material concern the shape of certain structures. Canter describes the sporangia of *Z. melosirae* as ovate and those of *Z. planktonicum* as obpyriform. In the Michigan fungus the sporangia on all three hosts were found to be distinctly obpyriform (Fig. 1 C, D, H, M), although occasionally those on *Asterionella* and *Synedra* had wide bases which gave them an almost spherical appearance (Fig. 1 C, D, H). Other differences in shape were found by Canter in the resting spores. She described those of *Z. melosirae* as ovate and *Z. planktonicum* as subspherical to oval. Although none were observed on *Melosira* in the present investigation, they were found on *Asterionella* and *Synedra*, and were spherical, oval or ovate (Fig. 1 F, I, J).

The nature of the rhizoidal system was found to be of particular interest in making a comparison of these organisms with Canter's. In the English material rhizoids of *Z. melosirae* were found to be sparingly or not at all branched, whereas in *Z. planktonicum* they were richly branched. Rhizoids in the present study were of variable character in each of the three hosts. They ranged from a single tube which was swollen terminally with a small uft of rhizoids in *Asterionella* sp. (Fig. 1 I), to a much branched rhizoidal ystem in *Synedra* sp. and *Melosira* sp. (Fig. 1 C, D, F, K, L, M).

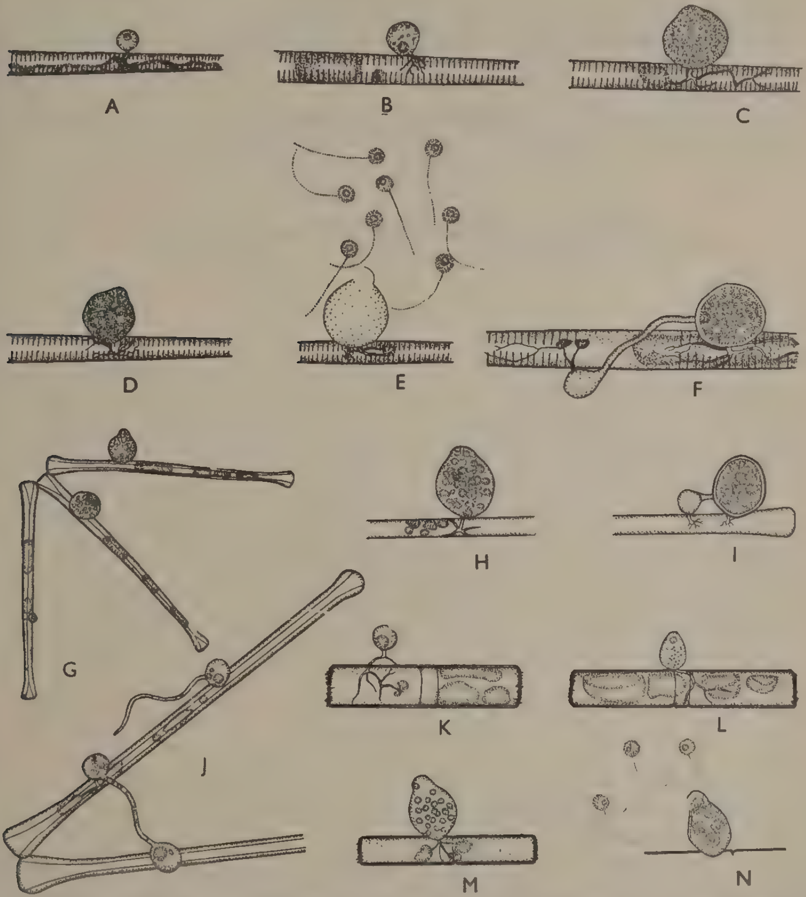

Fig. 1. A–F, *Zygorhizidium melosirae* Canter on *Synedra* sp.: A–D, stages in the development of the thallus; E, discharged operculate sporangium, the liberated zoospores about to disperse; F, sexually formed resting spore with smaller empty male thallus attached by its conjugation tube. G–J, *Z. melosirae* on *Asterionella* sp.: G, developing thalli on host; H, nearly mature sporangium; I, sexually formed resting spore with conjugation tube and empty male thallus; J, sexual stage showing two male thalli with conjugation tubes, one fused with a female thallus, the other unattached. K–N, *Z. melosirae* on *Melosira* sp.: K, L, early stages in thallus development; M, mature sporangium; N, discharging sporangium with zoospores. (A–F, H–N, ×925; G, ×382.)

Because of the similarities in the size and shape of structures, and in the variable nature of the rhizoidal system on all three hosts, *Z. planktonicum* is here considered to be the same as *Z. melosirae*. However, it is not necessary to reduce *Z. planktonicum* to synonymy since it has never been validly published.

I am grateful to Prof. F. K. Sparrow for his guidance during the course of this investigation.

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SEXUAL REPRODUCTION AND VARIATION IN *GLOEOTINIA TEMULENTA* (PRILL. & DELACR.) WILSON & GRAY

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(With Plate 26 and 1 Text-figure)

Gloeotinia temulenta has been shown to be obligately heterothallic and the evidence presented indicates that there are two mating types. Apothecia develop from ascogonial stromata which have been fertilized by microconidia from a compatible strain and mating between compatible strains is facilitated by the frequent infection of seeds by more than one strain of the fungus. Variation in the fungus as assessed on the basis of cultural characters is enormous and comparable with that found in such fungi as *Venturia inaequalis* and *Ustilago maydis*. Investigation of the conidial and mycelial strains reported by Wilson, Noble & Gray (1945) has shown that these strains are not sharply defined; expression of the conidial-mycelial character is under the control of more than one pair of alleles and is also affected by the nature of the substrate. A study of fifty isolates of the fungus showed no differences in nutritional requirements; all were biotin dependent and partially aneurin dependent.

Introduction

The discomycete *Gloeotinia temulenta* (Prill. & Delacr.) Wilson & Gray produces in rye-grass (*Lolium* spp.) the condition known as blind seed disease. The broad outlines of the life history of this organism were determined by Neill & Hyde (1939), and this work was later confirmed and elaborated by Wilson *et al.* (1945), Calvert & Muskett (1945), Corkill (1952), Neill & Armstrong (1955) and Wright (1956). These workers have shown that developing seeds of rye-grass are infected at flowering time, primary infections being produced by ascospores. Large numbers of conidia are formed during the early stages of infection and these produce secondary infections. When sown, infected seeds fail to germinate; they lie dormant over the winter and in the spring and early summer of the following year may produce microconidia and then apothecia and ascospores.

Several important aspects of this life cycle require further study. The mechanism of sexual reproduction has not hitherto been investigated nor is it known whether the fungus is homo- or heterothallic. Little is known of variation and, since satisfactory control of the disease in rye-grass appears to be dependent upon the development of resistant varieties, this is an important factor requiring consideration. Further, because all primary infections each year are by ascospores, the role of sexual reproduction in the initiation and perpetuation of genetic differences is of fundamental importance. Observations on these aspects of the life history are reported here.

MATERIALS AND METHODS

Seed samples

Samples of rye-grass seed from seed crops naturally infected with *Gloeotinia temulenta* were obtained principally from Northern Ireland, but a few samples were also obtained from Scotland, Wales and New Zealand. Infected seeds in these samples were detected by microscopic examination of the caryopses (Muskett, 1948).

Production of apothecia

No method is at present available for the production of apothecia in artificial cultures, and consequently all apothecia studied were obtained from either naturally or artificially infected seeds. Neil & Hyde (1942) observed that infected seeds could be induced to produce apothecia by placing them on moist sand in a refrigerator at 3–4° C. for 1 month or up to 4 months and then exposing them to light at laboratory temperatures. In the present investigation, it was found that, at about 2° C., a period of 8 weeks was necessary to produce the maximum crop of apothecia; no apothecia were produced with cold periods of 4 weeks or less and only a few after 6 weeks; longer cold treatments of 10 and 12 weeks duration produced no significant effects on apothecial production. Apothecial production generally began 4 weeks after removing seeds from the refrigerator and ceased after 8 weeks. All observations on the number of seeds producing apothecia were therefore based on a standard cold treatment of 8 weeks followed by 8 weeks at room temperature.

Isolation of the fungus in culture

The fungus was isolated directly from the mycelium in infected caryopses by the method of Muskett (1948) and from ascospores as follows: a suspension of ascospores was prepared by gently squeezing an apothecial disk in *c.* 1 ml. sterile distilled water; four drops of sterile water were placed on the surface of an agar plate and to each was added one loopful of the spore suspension. The drops were then streaked over the surface of the agar with a glass spreader and the individual ascospores, now well distributed, were picked off with the aid of a dummy objective. In order to study genetical segregations it was necessary to isolate the eight spores from several asci, and the following technique was adopted. A ripe apothecium was teased in a small quantity of sterile water; small tufts of asci were removed with a fine glass needle and transferred to agar-filmed coverslips, the asci being placed at the edge of the agar film. The coverslip was inverted on a wax Van Teighem cell and, using a Prior micromanipulator, a small group of asci (containing not more than two or three mature asci) was pulled away from the main mass so that it was well isolated from any loose spores. The mature asci were orientated so that their tips pointed toward the clear area of the agar film. The coverslip was then transferred to a ring slide containing a few drops of sterile water. Six such coverslips were usually prepared from a single apothecium. Some of the asci isolated in this way burst, discharging their ascospores in a group which lay a short distance from the mouth of the ascus (Pl. 26, fig. 6). The individual spores could be separated with the aid of the micromanipulator and their position on the agar film marked by means of an ink dot on the upper surface of the coverslip. Using the ink dots as a guide, portions of agar, each containing a single ascospore, were cut out with a small scalpel and transferred to slants of nutrient agar.

Culture media

The following media were used: 'Difco' corn meal agar, 2 % malt agar, and 'complete' medium (Pontecorvo, 1949). For studies on nutritional requirements a minimal medium (Pontecorvo, 1949) was also employed.

Determination of nutritional requirements

The auxanographic method (Pontecorvo, 1949) was used for part of this work. Spores from 7- to 10-day-old cultures were suspended in sterile distilled water. The suspension was centrifuged, the supernatant discarded, and the spores resuspended in sterile distilled water. This was necessary to remove contaminating nutrients present in the conidial slime. The concentration of the spores was adjusted to approximately 10^6 spores/ml. Tubes containing 15 ml. minimal medium were heated to melt the agar and cooled to 50° C. in a water bath. One ml. washed spore suspension was added aseptically to a tube of the medium and the contents poured quickly into a Petri dish. The plates were incubated for 24 hr. to allow the spores to germinate, and pieces of filter-paper soaked in the nutrients to be tested were placed on the surface. The plates were incubated for a further 7 days at 20° C. and the areas where growth occurred were noted. This method proved useful for determining absolute growth requirements; it was less useful, however, for determining partial requirements, and for such studies series of special synthetic media (minimal plus various growth substances) were used.

Artificial infection of rye-grass plants

Many workers have experienced difficulty in the artificial infection of rye-grass with *G. temulenta*. Wright (personal communication, 1954) found that the best technique was to immerse heads of rye-grass at peak flowering in a dense suspension of conidia, and this method was adapted to the present circumstances. The plants used consisted of divots taken from a pure stand of S24 rye grass in the autumn and potted up in 7 in. pots, which were brought into the glasshouse in the spring. Conidial suspensions were prepared from 7- to 10-day-old cultures grown on complete medium. The concentration of spores was adjusted to approximately 10^6/ml. and sufficient suspension was prepared to fill a 100 ml. measuring cylinder.

Plants were inoculated when 10–15 heads were present with the lower florets at anthesis. Young heads and heads which had begun to set seed were removed and the remaining flowering heads were immersed for 1 min. in the conidial suspension. Immediately after inoculation the heads were enclosed in a parchment pollinating bag and the plants placed in a moist atmosphere for 24 hr. They were then returned to the glass-house bench and the seed allowed to mature. The enclosure of the inoculated heads in a pollinating bag was considered necessary to minimize the risk of cross infections by different strains of the organism.

OBSERVATIONS AND EXPERIMENTAL RESULTS

Sexual reproduction

The present studies have shown that, under the conditions employed, relatively few seeds infected by *G. temulenta* produce apothecia. This may be illustrated by reference to three samples which were critically investigated. The seed of each sample was carefully screened to remove husks and foreign material and three lots of 200 seeds were then taken from each sample and subjected to the standard cold treatment to induce apothecial development. During the period at room temperature observations were made on the number of seeds which germinated, the number which produced microconidial pustules and the number which produced apothecia. At the end of the experiment seeds which had neither germinated nor produced either microconidia or apothecia were examined microscopically for infection by *G. temulenta* (Table 1).

Table 1. *Production of apothecia by seeds of rye-grass infected with* Gloeotinia temulenta

Sample		No. infected seeds (out of 200)	No. infected seeds with apothecia	%	Mean	No. infected seeds with microconidia
S24 (R28)	*a*	90	6	6·7	8·2 ± 1·72	0
	b	124	7	5·6		0
	c	113	14	12·4		0
Devon Eaver (R47)	*a*	40	3	7·5	7·3 ± 1·25	1
	b	44	2	4·5		0
	c	51	5	9·8		0
Irish Commercial (R56)	*a*	132	16	12·1	20·1 ± 3·31	5
	b	88	22	25·0		8
	c	73	17	23·3		0

Apothecial production is significantly greater in R56 than in R28 or R47, but there is no significant difference between R28 and R47.

In each sample only a relatively small proportion of infected seeds produced apothecia and very few seeds produced microconidia; indeed in several of the dishes no microconidia were observed. Similar results were regularly obtained in other samples of seed and apothecial production (expressed as percentage ungerminated seeds) was found to vary from 5 to 30%.

The low frequency with which infected seeds produced apothecia clearly required further examination. Formation of apothecia in the apparent absence of microconidia led, initially, to the view that microconidia might not be essential for apothecial production. Consequently, attention was focused on differences which were known to occur amongst nfected seeds. In isolating the fungus from seeds it had been noted that some seeds gave rise to sectored colonies (Pl. 26, fig. 1). At first this was attributed to mutation, but it soon became evident that this could hardly account for (*a*) the high frequency with which sectored colonies were found, and (*b*) the fact that sectors always originated from the seed itself. Were the occurrence of sectors to be explained on the assumption that the fungus was highly mutable then a proportion of the sectors would be expected to occur at some point away from the seed. Also, sectoring could not in this instance be attributed to dissociation of a heterokaryon since all the cells of the fungus are uninucleate (Griffiths, unpublished). The inference was therefore drawn that sectored colonies developed from seed which had been originally infected by more than one strain* of the fungus.

These observations, coupled with the knowledge that naturally occurring apothecia are regularly hybrid (see p. 471), led to the formulation of the following working hypothesis which contained two propositions: (1) that the fungus is heterothallic; (2) that mating between compatible strains may be accomplished by hyphal fusion.

The heterothallic nature was inferred from the regular occurrence of hybrid apothecia; the proposition that mating might occur by hyphal fusions arose from the finding that apothecia developed in the apparent absence of microconidia.

If both of the propositions were true then apothecial production would be restricted to seeds carrying compatible strains. Further, if the number of strains present in the seed rarely exceeded two (and it was never possible to detect more) then the proportion of seeds producing apothecia would, as shown later, provide information about the mating system.

Certain unusual features of *G. temulenta* enabled this hypothesis to be tested experimentally. The fungus exists as an apparently infinite number of strains distinguishable from one another by variations in cultural characteristics (see p. 473). Differences are not always large, but are sufficient for strains to be distinguished when growing alongside one another on the same plate. Consequently, there appeared to be good grounds for believing that seeds carrying more than one strain of the fungus could be detected.

Three groups of samples each containing three samples (i.e. nine samples in all) were investigated. The groups were studied on different occasions but every effort was made to ensure uniformity of conditions.

The proportion of infected seeds producing apothecia was determined on 1000 seeds taken from each sample. The proportion of seeds infected by more than one strain of the fungus, i.e. the proportion yielding sectored colonies, was determined in the following way. Seeds from each sample were dehusked and the caryopses examined microscopically for infection by *G. temulenta*. Fifty infected caryopses from each were then surface sterilized and, after bisecting, plated (four per plate) on 'complete' medium. The plates were incubated at 20° C. Not all the seeds produced colonies (see Pl. 26, fig. 1) and some of the plates were spoiled by contamination; consequently, additional infected caryopses were plated from each sample to bring the total number of isolations to over fifty per sample. The occurrence of sectored and homogeneous colonies was determined after 21 days. In many cases sectored colonies could be determined without difficulty by visual inspection (see, for example, Pl. 26, fig. 1). Other cases presented more difficulty, and in all cases where any doubt existed four mono-spore cultures were prepared from each presumed sector and grown on slants of complete medium. Comparison of cultures obtained from different sectors enabled the homo- or heterogeneity of the colony to be determined without difficulty.

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* The term *strain* is used here to denote any clone of the fungus which can be distinguished on cultural, morphological or physiological characteristics.

The relationship between the proportion of infected seeds producing apothecia and the proportion yielding sectored colonies was examined by the following method, for which I am indebted to Dr Alan Durrant who provided all the formulae employed.

The experimental results are shown in Table 2. If q is the proportion of infected seeds yielding sectored colonies and f is the proportion of those that produce apothecia and the various classes are represented as in Table 2*a*, then the maximum likelihood solutions for f and q are

$$f=\frac{a_1 n}{b_1 m}, \qquad q=\frac{b_1}{n};$$

and their variances are

$$V_f=\frac{f[n(1-fq)+mf(1-q)]}{mnq}, \qquad V_q=\frac{q(1-q)}{n}.$$

Table 2. *Production of apothecia and sectored colonies from seeds of rye-grass infected by* Gloeotinia temulenta

Group	Sample	No. infected seeds with apothecia	No. infected seeds without apothecia	Total	No. seeds yielding sectored colonies	No. seeds not yielding sectored colonies	Total
I	S24 (R53)	133	468	601	22	34	56
	S24 (R52)	110	370	480	24	33	57
	S24 (R48)	156	412	568	24	28	52
II	Devon Eaver (R12)	54	223	277	12	39	51
	Devon Eaver (R21)	37	154	191	9	43	52
	Devon Eaver (R38)	45	184	229	7	49	56
III	Hunsballe Sildig (R I)	35	215	250	20	36	56
	S24 (III)	67	319	386	24	38	62
	Irish Commercial (RIX)	40	366	406	18	45	63
	Total	677	2711	3388	160	345	505

Table 2*a*

	Seeds with apothecia	Seeds without apothecia	Total	Seeds with sectored colonies	Seeds without sectored colonies	Total
Numbers obtained	a_1	a_2	m	b_1	b_2	n
Expected proportions	fq	$1-fq$	1	q	$1-q$	1

Table 2*b*

Group	Sample	*f*	*q*
I	R53	0·5633 ± 0·1030	0·3929 ± 0·0656
	R52	0·5443 ± 0·1300	0·4211 ± 0·0656
	R48	0·5951 ± 0·1269	0·4615 ± 0·0693
II	R12	0·8285 ± 0·1546	0·2353 ± 0·0583
	R21	1·1193 ± 0·3768	0·1731 ± 0·0529
	R38	1·4672 ± 0·5568	0·1250 ± 0·0447
III	RI	0·3920 ± 0·0933	0·3571 ± 0·0640
	RIII	0·4484 ± 0·0872	0·3871 ± 0·0616
	RIX	0·3448 ± 0·0860	0·2857 ± 0·0566
Total		0·6307 ± 0·0583	0·3168 ± 0·0200

Table 2*c*

Component	Degrees of freedom	χ^2
Within group I	2	0·74
Within group II	2	13·30**
Within group III	2	2·12
Between groups	2	93·09
Total	8	109·25***

** Significant at 0·01. *** Significant at 0·001.

The values of *f* and *q* (together with their standard errors) are given in Table 2*b*. The values of *f* are estimates of the *proportion* of doubly infected seeds producing apothecia, and thus reflect the chances of any two genotypes being compatible. If, as in all other ascomycetes investigated, only two mating types are involved (Lewis, 1954) then one half of the seeds which were doubly infected would be expected to contain compatible strains, that is the values of *f* should not depart significantly from 0·5. From Table 2*b* it can be seen that although the values of *f* vary considerably none depart significantly from this value. The estimate of *f* for the combined data, however, shows a significant departure. This estimate, based on a much larger number, is a more rigorous test, but is only admissible if there is no significant heterogeneity in the data. Inspection suggests that this is unlikely and has been confirmed by the following analysis.

An estimated mean value of *f* for all or any part of the data can be calculated from

$$f' = \frac{1}{\Sigma m}\Sigma\frac{a_1}{q},$$

where the contribution of each sample is weighted according to the size of the sample (m) and corrected by the corresponding value of q. A χ^2 testing heterogeneity is then given by

$$\chi^2 = \Sigma\frac{(a_1 - f'qm)^2}{(1 - f'q)\,f'qm}.$$

The results of this analysis are shown in Table 2*c*. The total heterogeneity is very high indeed, but it is clear that it lies almost entirely between groups of samples. Within each group it is small and only in one case is it significant at the 0·01 level.

Considering the analysis as a whole there is support for the view that only half of the seeds carrying two strains of the fungus produce apothecia. The analysis of heterogeneity shows, however, that some factor or factors are influencing the results, and further that this influence operates principally on experiments performed at different times. There is no *a priori* reason for supposing that there are any intrinsic differences between the three groups of samples with regard to *f*, although we may well expect the groups to show differences in *q* since they have come from different populations. Hence it must be concluded that any differences must be attributed either to variation in the environmental conditions or to variation in technique. Every effort was made to maintain strict uniformity in the techniques used and the only major variable factors are the conditions under which apothecia develop following cold treatment of the seed. It will be recalled that apothecia were allowed to develop in Petri dishes on the laboratory bench. While the samples within any one group would be exposed to the same environmental conditions, each group would be subjected to somewhat different conditions since the groups were examined at different times. In view of the results obtained in the following experiments, these differences in environment may well account for the variation found.

Using the four genotypically different strains from one ascus (designated A, B, C and D) it was hoped to produce, by artificial inoculation, ten seed samples infected with pure strains and combinations of strains as follows: A, B, C, D, A+B, A+C, A+D, B+C, B+D, C+D. Such seed could then be used for several experiments: (i) to check the findings of the previous experiment; (ii) to provide a precise demonstration of the heterothallic nature of the fungus and its mating system; (iii) to provide further information concerning the mechanism whereby mating between strains occurred. This latter point was considered important particularly in view of the results obtained with the samples in group 2 in the last experiment. These showed a large excess of apothecia over that expected on the basis of the occurrence of sectored colonies. Provided that this latter value was not a gross underestimate, then a proportion of the apothecia must have arisen from seeds carrying only one strain of the fungus which had in some way been 'fertilized'. This could presumably have been accomplished by microconidia and it was hoped to examine this point further.

The four strains from one ascus (Pl. 26, fig. 2) were used and the inoculations carried out using the technique described under Materials and Methods. When ripe, the inoculated inflorescences were harvested and threshed and the total number of seeds obtained are shown in Table 3. Before proceeding with further experiments it was clearly important to obtain some information about the numbers of seed in each sample which were actually infected. Ten seeds from each sample were examined; infected seeds were found in five samples but in only three was more than one seed found to be infected (Table 3). Because of this low degree of infection it was evident that insufficient seeds would be available to etermine the proportion of double infections in those samples which had een originally inoculated with a mixture of two strains. Consequently ll the seed was subjected to the standard cold treatment for inducing pothecial production.

During the period at room temperature seeds which germinated were iscarded. The numbers of ungerminated seeds are shown in Table 3.

Table 3. *Numbers of infected seeds produced in inoculation experiment*

Inoculum ...	A	B	C	D	A+B	A+C	A+D	B+C	B+D	C+D
otal numbers of seeds harvested	609	563	412	237	464	182	512	307	265	325
umbers of infected seeds found in sample of 10	2	3	0	0	2	0	1	1	0	0
umbers of seeds which did not germinate	109	92	12	9	86	3	12	21	6	8
umbers of ungerminated seeds found to be infected	79	71	3	2	64	0	7	6	2	4

ailure of germination is not an absolute criterion of infection by *G. temu-enta*, but at this stage it was considered undesirable to risk damage to the ernels by removing the pales in order to determine which seeds were ctually infected. Consequently in designing the experiments ungermiated seeds were provisionally considered as infected. When the experiments had been completed the ungerminated seeds which had not shown hemselves to be infected (e.g. by producing apothecia) were dehusked and examined microscopically. The numbers ultimately found to be infected are given in Table 3.

Only seeds infected with strains A, B and A+B were available in sufficient numbers to test the possible function of microconidia. Five lots of ten seeds were placed on moist sand in a Petri dish, and 3 weeks after the seeds had been removed from the refrigerator, inoculation with microconidia was commenced. This time was chosen for the commencement of inoculation since this was the time when microconidia (when they occurred) were first found in samples of naturally infected seed. Dense suspensions of microconidia were prepared from cultures of each of the four strains and the inoculations carried out as indicated in Table 4. One drop of spore suspension was applied to each seed. After 7 days, signs

Table 4. *Numbers of seeds (out of 10) producing apothecia after inoculation with microconidia*

Seed	Microconidia A	Microconidia B	Microconidia C	Microconidia D	Uninoculated control
A	0	0	7	7	0
B	0	0	7	8	0
A+B	0	0	9	8	0

of apothecial development were observed on seeds in some of the dishe and after 14 days it could be seen that:

(*a*) uninoculated seeds produced no apothecia;
(*b*) selfs (i.e. A × A and B × B) produced no apothecia;
(*c*) crosses between A and B produced no apothecia;
(*d*) crosses A × C, A × D, B × C and B × D produced apothecia.

Repeat inoculations were carried out at weekly intervals for a further 3 weeks but the results remained unchanged. Seeds which had not yielded apothecia from the fertile crosses were found on inspection at the end o the experiment to be uninfected.

It was noticed that in the fertile crosses apothecia began their development in many cases from small groups of pear-shaped structures covered with fine hair-like hyphae (Pl. 26, fig. 5). These structures were presumed to contain the ascogonia of the fungus and are referred to here as 'ascogonial stromata'. As soon as the significance of these structures was noted (7 days after the first inoculations with microconidia) a subsidiary experiment was set up to determine whether apothecial production was dependent upon the presence of ascogonial stromata. Examination of the seed remaining in samples infected with strains A and B showed twenty-seven seeds with ascogonial stromata in A and only twelve in B. These were divided into two groups as indicated in Table 5 and matched with an equal number of seeds not showing ascogonial stromata. Microconidia from strains C and D were used for inoculation and the results are shown in Table 5.

Table 5. *Numbers of seeds, with and without ascogonial stromata, producing apothecia after inoculation with microconidia*

		Microconidia			
		C		D	
		No. inoculated	No. prod. apothecia	No. inoculated	No. prod. apothecia
A	+asc. str.	14	14	13	13
	−asc. str.	14	4	13	5
B	+asc. str.	6	6	6	6
	−asc. str.	6	2	6	3

Where ascogonial stromata were present all seeds yielded apothecia; where they were absent only a few seeds produced apothecia. Subsequent inspection revealed that where no ascogonial stromata were observed the apothecia developed from the region between the pale and the caryopsis, and it was inferred that ascogonial stromata might also be produced in this position. This finding led to a re-examination of the distribution of microconidia, and a study of sections of infected seeds showed that in many cases small microconidial sporodochia were present also between the pales and the caryopsis. The significance of this is discussed later.

These experiments with microconidia showed clearly that the fungus is heterothallic; unless compatible strains are present no apothecia are produced. Further, it would appear that two mating types are present;

in the present instance strains A and B belong to one mating type and C and D to the other. It was anticipated therefore that seed which had been originally infected with compatible strains might produce apothecia (i.e. from flowering heads inoculated with strains A+C, A+D, B+C and B+D). No apothecia were produced in any of these samples though the seed was kept for 12 weeks after removal from the refrigerator. However, neither microconidia nor ascogonial stromata were observed on any of these seeds and inspection at the end of the experiment showed that only a small number were actually infected.

Variation

An initial survey of variability in *G. temulenta* was made using a number of seed samples from different sources (Table 6). The samples were cold-treated and five out of seven yielded some apothecia. Ten ascospores were isolated at random from each of three apothecia in each sample. The spores were placed on slants of 'Difco' cornmeal agar and incubated at 20° C. Not all the spores grew and produced colonies, but eighty cultures were obtained from the 130 ascospores isolated. Subcultures of all isolates were made to 2 % malt agar, 'complete' medium, and 'Difco' cornmeal agar.

Table 6. *Growth characteristics of mono-ascospore isolates of* Gloeotinia temulenta

Sample No.	Country of origin	Host species and strain	No. of apothecia studied	Apothecium No.	No. of cultures obtained	Growth characteristics on 2 % malt agar		
						C	CM	M
1	N. Ireland	*L. perenne* S24	3	1	8	0	8	0
				2	6	1	4	1
				3	4	0	2	2
2	N. Ireland	*L. perenne* Devon Eaver	1*	4	7	2	5	0
3	Scotland	*L. perenne*	3	5	2	0	2	0
				6	8	0	8	0
				7	8	0	5	3
4	N. Zealand	*L. perenne*	3	8	7	0	4	3
				9	4	1	1	2
				10	3	0	1	2
5	N. Zealand	Short rotation rye-grass	3	11	9	1	6	2
				12	7	2	4	1
				13	7	0	3	4

* Only one apothecium produced.

All isolates showed differences in cultural characters on all three media but in addition each medium exerted a pronounced overall effect on the growth of the isolates. Thus on Difco cornmeal agar, growth of all isolates was generally weak and spore production poor; no aerial mycelium was produced and the colour of the colonies ranged from very pale cream to fawn. On 'complete' medium, much better growth was obtained; initially the colonies were various shades of light brown, and conidial production was abundant so that an oily streak which ran down the agar slant was usually produced; all cultures darkened with age; small amounts of aerial mycelium were produced in some cultures. On 2 % malt agar, growth was more like that on 'complete' medium except that conidial production was more variable; aerial mycelium was generally more abundant and on this medium three broad classes of cultures could be distinguished:

(*a*) Conidial (C)—cultures producing sufficient conidia for slime to be produced and to run down the slant, forming a streak.

(*b*) Conidial-mycelial (CM)—cultures with abundant conidia but not sufficient for the slime to form a streak; aerial mycelium varying from slight to abundant.

(*c*) Mycelial (M)—cultures with no conidial slime and few spores; aerial mycelium abundant.

These categories are arbitrary and grade imperceptibly into one another. Their occurrence in the eighty isolates is shown in Table 6. In general, conidial strains are infrequent, most cultures being either mycelial or conidial-mycelial. There was no evidence of differences which could be attributed to the country of origin of the seed samples in the conidial-mycelial character or indeed in any of the other cultural characters.

Segregation for conidial and mycelial strains appeared to be occurring in the apothecia studied, and this segregation was examined further in a comparison of the cultures obtained from the eight spores in individual asci. When the eight ascospores were isolated from a single ascus and grown in culture, the colonies were found always to fall into four pairs, the members of each pair having identical cultural characteristics. These pairs were clearly derived from the final mitosis in the ascus, and would thus be genotypically identical. For convenience, only one member of each pair was maintained in culture. The results obtained with eight asci are shown in Table 7.

Segregation of mycelial and conidial strains was found in five asci but the segregation pattern is not a simple one and evidently more than one pair of genes is involved in the expression of this character. It seems possible that a considerable number may be involved, since the variation from

Table 7. *Segregation of conidial and mycelial strains in eight asci of* Gloeotinia temulenta

		Strain			
Apothecium	Ascus	A	B	C	D
I	(*a*)	C	C	C	C
	(*b*)	C	C	C	C
II	(*a*)	C	CM	CM	CM
	(*b*)	CM	C	CM	C
III	(*a*)	C	CM	M	M
	(*b*)	M	M	CM	CM
IV	(*a*)	C	CM	M	CM
	(*b*)	M	M	M	M

All apothecia were from a single sample of infected seed (S24) from Northern Ireland. The letters A, B, C, D, designate the four strains obtained from each ascus.

xtreme conidial to extreme mycelial is apparently continuous (Pl. 26, ig. 3). This is brought out more clearly in a study of the progeny from rosses between strains where the behaviour of the parents was known.

Apothecia derived from four different crosses were available—A × C, × D, B × C and B × D (see Table 4). From each cross two apothecia vere selected at random and thirty ascospores were isolated from each, nd grown on slants of 2 % malt agar at 20° C. The cultures obtained vere classified as conidial, conidial-mycelial or mycelial (Table 8). Of the 97 cultures obtained, eleven were conidial and the remainder fell approximately equally into the conidial-mycelial and mycelial groups. There vere, however, highly significant differences between the crosses as shown y a heterogeneity χ^2 analysis (Table 8*a*). Crosses involving strain A as

Table 8. *Cultural characteristics of progeny from crosses between mono-ascospore lines*

Cross		Apothecium	Progeny		
			Conidial	Conidial-mycelial	Mycelial
A × C	Type 1	(i)	2	14	10
		(ii)	3	15	6
A × D		(i)	2	15	9
		(ii)	0	14	9
B × C	Type 2	(i)	1	9	14
		(ii)	1	5	18
B × D		(i)	1	12	11
		(ii)	1	9	16

Table 8*a*. *Heterogeneity χ^2 analysis of data in Table 8*

Component	χ^2	Degrees of freedom	Probability
Types	14·1764	1	0·001
(Crosses	14·6614	3	0·001)
Between crosses within types	0·4868	2	0·800
Within crosses	8·3315	4	0·050
Total	22·9947	7	0·001

the ascogonial parent differed significantly from those with strain B as the ascogonial parent, there being a greater proportion of conidial-mycelial strains in the progeny from the former. There were, however, no other significant differences. This is perhaps not surprising, since the only major difference between the strains was that strain A was conidial whereas the other three strains were conidial-mycelial. There is evidence here for the inheritance of the conidial-mycelial character, but it is clear that the inheritance is complex.

The conidial-mycelial character has been considered in some detail since attention has been drawn to it by other workers (Wilson *et al.* 1945). However, practically all other cultural characters show a similar range of variation. These characters (colour, colony margination, texture, etc.) are even less amenable to categorization. Each mono-ascospore isolate appears to represent a distinct genotype, since rarely are two identica cultures found.

Because of the difficulties involved in defining the variation in cultura characters shown by this fungus, attention was turned to the possibility of physiological differences. A search was made for differences in nutritional requirements, since it was hoped that these might be definable in more precise terms. Fifty isolates from various sources were selected for study. These were first tested by the auxanographic method for response to (*a*) yeast extract, (*b*) casein hydrolysate and (*c*) yeast nucleic acid. In every case there was a clear response to yeast extract but not to either casein hydrolysate or nucleic acid. Further, combinations of these three major nutrients showed no evidence of complementary requirements. The testing of the response of strains to various yeast 'factors' was then undertaken. Again all strains behaved similarly; there was a marked response to biotin but no clear response to any of the other substances tested singly. Examination of complementary requirements gave somewhat inconclusive results, though there were indications that aneurin in the presence of biotin gave an increased response. It was decided to explore this further and each of the fifty strains were grown on nine different media which contained, in addition to the basal nutrients (glucose plus mineral salts), the growth factors shown below:

	Medium								
	1	2	3	4	5	6	7	8	9
Nicotinic acid	+	−	−	+	+	−	+	−	+
Riboflavin	+	−	−	+	+	−	+	−	+
Aneurin	+	+	+	+	+	+	−	−	−
Biotin	+	+	+	+	+	+	+	+	−
p-Aminobenzoic acid	−	+	−	+	−	+	+	+	−
Pantothenic acid	−	−	+	−	+	+	−	+	+
Pyridoxine	−	−	+	−	+	+	−	+	+

The arrangements of the combinations of growth factors shown above does not enable all complementary deficiencies to be 'pin-pointed' precisely; it does, however, enable the complementary factors to be located in one of four groups.

Again the fifty strains behaved in the same way. Little or no growth was obtained on medium 9 which lacked biotin and relatively poor growth was obtained on media 7 and 8 (+biotin but lacking aneurin). On all the other media, which contained both aneurin and biotin, very good growth was obtained (Pl. 26, fig. 4). No differences in growth responses between the isolates were observed.

DISCUSSION

All heterothallic ascomycetes so far investigated have a two-type or bipolar mating system (Catcheside, 1951; Lewis, 1954) and the evidence available for *G. temulenta* indicates that a similar situation exists here also.

Experiments with microconidia have shown that they are functional in *G. temulenta* as they are in such related fungi as *Sclerotinia gladioli* (Drayton, 1934) and *S. convoluta* (Drayton, 1937). The results do not, however, preclude the possibility of mating by hyphal fusions when compatible strains are present in the same seed. Observations on seeds which have been cold-treated to induce apothecial formation have shown that 'visible' (i.e. superficial) microconidial sporodochia are rarely produced on infected seeds and that even in samples where they are absent apothecia may still be produced. However, the finding that ascogonial stromata might be produced between the pale and the caryopsis and hence concealed from view, led to a re-investigation of the occurrence of microconidia. In sections of several infected seeds small microconidial sporodochia were detected between the caryopsis and the pale. Hence there is no longer any evidence to support the original belief that apothecia might be produced in the absence of microconidia. If the alternative view is taken that all apothecia develop from ascogonial stromata fertilized by microconidia, reconsideration must be given to the results relating to the occurrence of doubly infected seeds and apothecial production. Evidently seeds infected by compatible strains have an important advantage compared to seeds not so infected. Even though only a few microconidia are produced, fertilization is very likely to occur, particularly if both ascogonial stromata and microconidia are produced in the small space between the caryopsis and the pale. Seeds not infected by compatible strains are, in contrast, unfavourably placed; they are dependent upon an external source of microconidia, i.e. microconidia from other infected seeds, and these, unless produced external to the seed, are unlikely to be disseminated very widely. However, where microconidia are relatively abundant, seeds not infected with compatible strains will certainly be fertilized and yield apothecia. In such cases the relationship, no. of apothecia $=\frac{1}{2}$ no. of doubly-infected seeds, will be seriously upset owing to an excess of apothecia. This appears to have occurred in the second group of samples tested (R 12, R 21, R 38). Moreover, as might be expected, the relationship between the occurrence of apothecia and the occurrence of doubly-infected seeds (expressed by the value f) shows considerable variation; a highly significant heterogeneity was found within this group of samples but not within the other groups.

Thus the results available are not in any way inconsistent with the alternative view that apothecial production is entirely dependent upon a supply of microconidia. Indeed, this provides the only really satisfactory explanation for the heterogeneity found in values of f (Table 2*c*). However, the possibility of fertilization by hyphal fusions remains, though it is difficult to see how this could be proved or disproved experimentally.

In view of the obligately heterothallic nature of the fungus and the fact that a sexual generation is interposed at the beginning of each season, it is not surprising that enormous variation has been found. Comparable variation has been found in other heterothallic species such as *Venturia inaequalis* and *Ustilago zeae*. In *V. inaequalis* Rudloff (1935) and Schmidt (1937) found that the number of strains was almost exactly proportional to the number of isolations made. Schmidt (1935) reported further that eight strains had been isolated from a single leaf. This latter observation is of particular interest in the present case. In *V. inaequalis* the female sexual organ consists of a coiled ascogonium equipped with a trichogyne but, unlike the situation in *G. temulenta*, the 'male' gametangium consists of a terminal cell of a hypha of opposite mating type. Clearly compatible strains of *V. inaequalis* must be present in the same leaf for fertilization and perithecial production to occur. It would be of obvious interest to know whether the proportion of leaves producing perithecia was related to the occurrence of multiple infections but no observations on this point appear to have been made. Similarly, widespread variation also occurs in *U. zeae*, maize smut, and this is considered later in relation to the problem of breeding resistant varieties.

Variation in cultural characters proved particularly difficult to study owing to the problem of categorizing the various forms. However, it was possible to investigate the occurrence and to some extent the inheritance of one pair of contrasting characters—conidial/mycelial. Wilson *et al.* (1945), who also observed the occurrence of conidial and mycelial strains, claimed that they were sharply defined and that these growth characteristics were independent of substrate. Neither of these claims are supported by the present observations. There is clearly a gradation from extreme mycelial to extreme conidial forms and further it was evident that substrate markedly affected growth characteristics. The progeny from crosses between parents of similar (CM × CM) and dissimilar growth forms (C × CM) showed in both cases a complete range of forms, indicating that the character is under the control of more than one pair of alleles.

Because of the wide variation encountered in cultural characteristics, it was anticipated that similar variation would be found in physiological characters. However, in the admittedly limited field of nutritional requirements, no differences could be detected, even in a very diverse sample of strains. No attempts were made to explore the possibility of variation in pathogenicity. In view of the difficulties encountered by Wright (1956) in establishing a standardized infection technique, this would clearly have constituted a major problem. Moreover, in view of the considerations to be presented later, it seems doubtful whether such work is really justified at the present time.

The problem of controlling blind seed disease has been discussed in some detail by Wright (1956) who has pointed out that four types of control techniques are available. These may be summarized as follows:

(1) Abandonment (for seed production) of areas where the disease is most severe and the use of areas where the disease does not occur, or is rare. This would provide a simple solution to the problem but, because of the serious economic and political implications, is unlikely to be adopted as a positive policy.

(2) Use of cultural practice along the lines advocated by Hardison (1948). These have proved eminently successful under the rather special conditions existing in Oregon but unfortunately are not applicable in Britain and New Zealand.

(3) The use of fungicides. Hair (1952) has obtained promising results under experimental conditions, but whether they can be applied on a field scale, at a sufficiently low cost, has not been established.

(4) Resistant cultivars. These, at present, offer the only satisfactory solution to the problem of disease control in Britain and New Zealand,

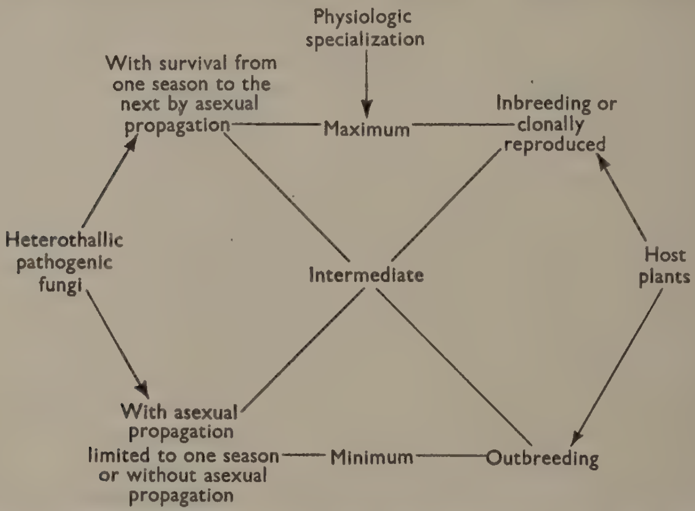
and because of this considerable attention has already been given to the selection of resistant clones.

In view of these considerations it is pertinent to ask whether the present observations have any practical implications for the plant breeder. Before attempting to answer this question, however, it is necessary to examine in some detail the various genetical relationships which may occur between fungal pathogens and their hosts.

Fungal pathogens vary considerably with regard to the range of hosts which they can invade. Thus at one extreme are organisms such as *Phymatotrichum omnivorum* which attacks some 2000 species of dicotyledons (Blank, 1953) and at the other extreme biotypes or races of such organisms as *Puccinia graminis tritici* which are restricted to a few cultivars (= genotypes) of *Triticum vulgare*. Clearly the relationship between host and parasite is much more delicately balanced in the latter case than in the former. It is not surprising, therefore, that small genetical differences in wheat may alter the 'host environment' so that it is no longer acceptable to a particular race of *P. graminis* and equally that major genetical changes in the host have no appreciable influence on susceptibility to *P. omnivorum*. Thus it would appear on *a priori* grounds that breeding for resistance would be easier in the case of *P. graminis* than in that of *P. omnivorum*. This is borne out by experience; no cultivars of cotton, for example, are known which show any resistance to *P. omnivorum* whereas in wheat it is relatively simple to provide a cultivar resistant to any particular race (the existence in *P. graminis tritici* of a very large number of races with different host ranges is a secondary problem of great complexity which should not be allowed at this stage to obscure the general argument).

It is important to appreciate the fact that the delicately balanced relationship between *P. graminis* and its host is dependent upon the ability of both host and pathogen to perpetuate particular genotypes indefinitely. Considerable attention has been given to the importance of mechanisms providing for greater variability in pathogenic fungi (e.g. Mather, 1942), but less emphasis has been given to the significance of mechanisms which ensure the survival of specific genotypes. If it is true that the highest degree of physiological specialization can only be achieved where the genotypes of both host and pathogen are maintained unchanged from one generation to the next, then any mechanism obligately imposing a measure of genetic variability in either pathogen or host, will reduce the extent of specialization. It becomes important, therefore, to examine the various relationships which may exist between pathogens and hosts as far as their genetic systems are concerned. The situations which may occur are discussed below and are summarized in Text-fig. 1.

The great majority of pathogenic fungi are capable of maintaining particular genotypes from one season to the next. Even in those species which are obligately heterothallic, survival of a favoured genotype is ensured by survival of asexual spores or mycelium (e.g. uredospores in rusts; conidia and mycelium in *Erysiphe graminis*). However, in obligately outbreeding organisms where survival is dependent upon the production of sexual spores, particular genotypes cannot be maintained intact for more than one season. Such situations are rare but where they do occur a marked reduction in host specialization is found. Gäumann (1950) goes as far as saying: 'If asexual propagative spores are lacking and every reproduction is a sexual one as in the pear rust, *Gymnosporangium sabinae*, then biotypes* cannot develop at all.' This appears to be an overstatement, inasmuch as members of the Ustilaginales which regularly undergo sexual reproduction prior to infection of each new host show evidence of physiological specialization. This is particularly true of the inbreeding cereals (e.g. wheat, oats) where, for example, twenty-five races of wheat bunt (*Tilletia caries*) are known and a similar number of races in the complex of *Ustilago* species attacking oats (Holton & Tapke, 1953). In these cases the perpetuation of host genotypes must be a potent factor in selecting physiological races. However, it should be stressed that physiological races in smuts and bunts are not sharply defined; they are, as pointed out by Stakman & Christensen (1953), 'collections of chlamydospores that behave with relative constancy in successive generations'. Because of sexual recombinations and mutations, however, they often comprise many genotypes, usually closely enough related so that the race behaves fairly constantly.


Physiologic specialization
With survival from one season to the next by asexual propagation
Maximum
Inbreeding or clonally reproduced
Heterothallic pathogenic fungi
Intermediate
Host plants
With asexual propagation limited to one season or without asexual propagation
Minimum
Outbreeding

Text-fig. 1. Interactions between the breeding systems of heterothallic pathogenic fungi and those of their hosts in relation to physiologic specialization.

Thus the argument that physiological specialization is reduced by factors which prevent the propagation of particular genotypes appears to be true as far as the pathogen is concerned. With outbreeding hosts a similar situation is found and a few examples will suffice. Striking examples of the effect of genetic heterogeneity in the host on physiological specialization are to be found in races of *Puccinia graminis* attacking rye and timothy (*Phleum pratense*). Only fourteen races of *P. graminis* have been recorded on rye (Stakman & Levine, 1935) as compared with 200 races on wheat.

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* The term biotype here is synonymous with strain as defined in the footnote on p. 465.

urther, Stakman & Levine (1934) noted that stem rust on rye was ‘more enerally distributed’ and that the physiological races of this variety P. *graminis secalis*) occurred more commonly on the weed grasses than did hose of either wheat or oats. This latter observation clearly indicates a uch lower order of specialization on rye as compared with either wheat r oats. On timothy, the rust *Puccinia phlei-pratense* (now considered a ariety of *P. graminis*) has been of sufficient importance to warrant selecon of resistant varieties and an examination of the fungus for physiological aces. Barker & Hayes (1924) found no evidence of physiological specialiation in this rust. Of even greater significance is the fact that resistant elections made over 20 years ago at Aberystwyth have remained resistant ven when grown in widely separated parts of the British Isles (Sampson & Vestern, 1954).

Before considering the situation where both the pathogen and host are egularly heterogeneous, mention should be made of the interesting ituation found in apple scab caused by *Venturia inaequalis*. This fungus is ighly variable (Rudloff, 1935; Schmidt, 1937) and has been shown by Keitt & Palmiter (1938) to be obligately heterothallic. Further, primary nfections each year are ascosporic, so that the situation closely resembles hat found in *G. temulenta*. The host, however, while a natural outbreeder nd consequently potentially heterogeneous, is now propagated clonally. There exist, thus, many cultivars (clones) each presenting the pathogen vith innumerable individuals of identical genotype. This situation is thus omparable with that of smut fungi on inbreeding cereals and it might be nticipated that some measure of physiological specialization would have ccurred. It is of particular interest, therefore, that Keitt, Lenen & Shay 1948) have already shown that monosporic lines may differ in pathogenicity. Further, these differences could be shown to be controlled by ingle loci. Thus pathogenicity to the varieties Haralson and Wealthy was ontrolled by one locus and pathogenicity to Yellow Transparent and McIntoch at another. There is, therefore, a basis for the development of physiological races of the kind encountered in smut fungi and clearly this must be taken into account in future work on the development of apple cultivars resistant to scab.

Examples of host-parasite relationships where both host and pathogen are regularly heterogeneous are, unfortunately, rare and only one case has been found where detailed information is available—that of *Ustilago maydis*, common smut of maize.

This fungus has been the subject of exhaustive studies because of its economic importance and because resistant cultivars have figured largely in control programmes, owing to the lack of effective cultural control practices. The organism is, like other species of *Ustilago* (Whitehouse, 1951), obligately heterothallic with two mating types. Infection is preceded by meiosis and the subsequent fusion of compatible sporidia to yield an infective dikaryon. Many workers have shown that the organism is immensely variable and certain strains appear to have an exceptionally high mutation rate. With this variability it is not surprising that Christensen (1929) was able to demonstrate that dikaryons varied in their ability to infect particular cultivars of maize. This result, however, has little significance for the problem of breeding resistant cultivars; as with any heterogeneou population some individuals will fail to thrive in a particular environment what is much more important is that the population as a whole contain individuals capable of fitting in to a wide range of niches. No cultivars o maize immune to smut have been produced, but lines with a high degre of resistance have been developed. Hayes, Immer & Smith (1955) summarizing the work on breeding for resistance to smut, state: 'Variou workers have found it relatively easy, however, to select inbred line resistant to smut, from crosses between resistant and susceptible inbred and from selection in self-pollinated crosses in commercial varieties *Resistance seems to be relative and probably functions under normal condition against all physiologic races of smut'* (italics mine).

This summation of the work on breeding resistance to *Ustilago maydis* i maize is of great interest, since it reveals the essential nature of the situation; maize smut behaves as a relatively unspecialized pathogen an resistance appears to depend on some general character of the plant Immer (1927) and Hoover (1932) noted associations between susceptibilit and tassel seed, brachytic and liguleless, and Hayes *et al.* (1955) hav suggested that the nature of the association may be explained on the basi that the morphological character tends to make the plant more susceptible

Experience with *Ustilago maydis* and with potentially highly specialize parasites such as *Puccinia graminis* on outbreeding crops such as rye an timothy have obvious and important implications for the problem o producing cultivars of rye-grass resistant to *Gloeotinia temulenta.* Despite the variability which has been found in the fungus, it appears unlikel that marked physiologic specialization will occur. Resistance is also likel to function against all strains, and is moreover likely to be stable. Work has been in progress for too short a while for it to be possible to asses whether these predictions are likely to be upheld. However, the lack o immunity in any clone of rye-grass so far tested (Corkill, 1952; Wright, 1956) is indicative of a relatively low degree of specialization, and it i encouraging that plants with a fairly high degree of resistance have already been found in agronomically valuable cultivars of rye-grass (Corkill, 1952; Wright, 1956).

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EXPLANATION OF PLATE 26

Fig. 1. Colonies of *Gloeotinia temulenta* developing from infected caryopses after 21 days at 20° C The colony on the left shows the sectored type; that on the right the homogeneous type Two caryopses from which no mycelium has grown are also present (×0·5).

Fig. 2. The four genotypically different strains (A, B, C and D: top left, top right, bottom lef and bottom right, respectively) from ascus II (*a*), Table 7 (×0·5).

Fig. 3. Mono-ascospore isolates from the cross B × C grown on 2% malt agar at 20° C. fo 21 days. Isolate 1 is mycelial; isolates 2, 3 and 4 are mycelial/conidial; isolates 5 and 6 ar conidial. Note that the production of conidial slime increases steadily from isolates 2 to 6 (×0·5).

Fig. 4. Typical behaviour of an isolate of *G. temulenta on* (*a*) minimal plus aneurin and biotin (*b*) minimal plus biotin but minus aneurin and (*c*) minimal (×0·5).

Fig. 5. Ascogonial stromata and very young apothecia of *G. temulenta*. The seeds with apothecia were inoculated 7 days previously with microconidia (×0·5).

Fig. 6. The eight ascospores of *G. temulenta* lying at the mouth of the ascus prior to separatio by micromanipulator (×500).

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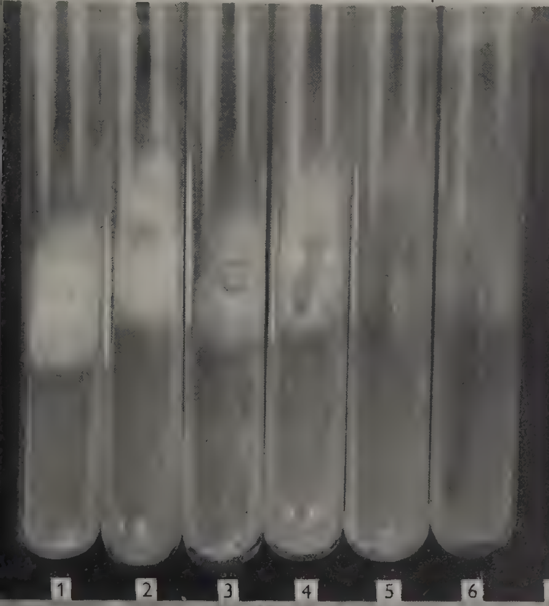

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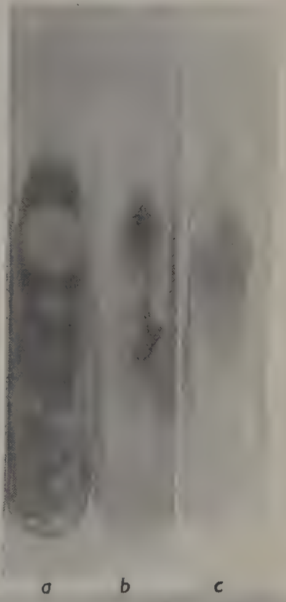

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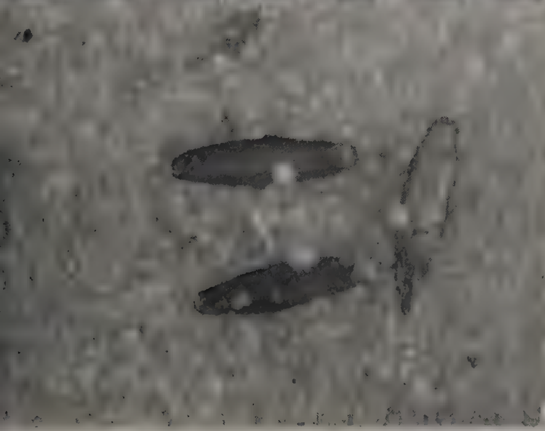

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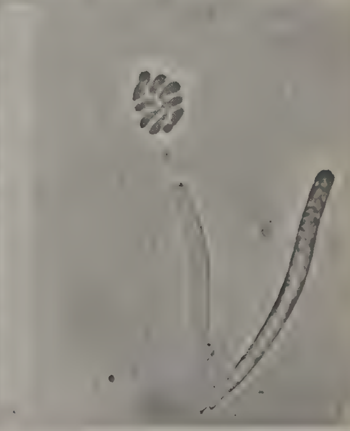

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Trans. Brit. mycol Soc. **41** (4), 483–490 (1958).

INFLUENCE OF pH ON THE INCIDENCE OF DAMPING-OFF

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(With 1 Text-figure)

Using *Beta vulgaris*, *Brassica campestris*, *Picea sitchensis* and *Pinus contorta* as hosts, *Pythium ultimum* as parasite, and a wide range of soil reactions, it is shown that change in incidence of damping-off with chnge in soil pH is strongly negatively correlated with change in growth rate of the host. No corresponding positive correlation with the fungal growth rate nor, with one exception, with the parasite/host growth rate ratio, was demonstrated.

INTRODUCTION

Garrett (1956) stated that: 'The parasites causing pre-emergence killing, damping-off and seedling blights of seedlings are certainly primitive parasites by any definition....There are good reasons for supposing that most seedling parasites are, like *Pythium* species and *Rhizoctonia solani*, aprophytic sugar fungi....In each case there is a race with time; in one ase the race is against competitors for colonization of an ephemeral ubstrate, and in the other against maturation of young and susceptible host tissues.'

If this is so, the damping-off diseases should provide excellent material or the study of simple concepts in plant pathology, in particular the concept that the relation between incidence of the disease and a physical nvironmental factor will depend, at least in part, on the influence of that actor on the growth rates of both host and parasite. Such a concept, esting as it does on the postulates that pathogenicity and resistance are elated to the growth rates of parasite and host, respectively, could only be demonstrated in the case of simple necrotrophic parasites.

Hawkins & Harvey (1919) and McClure & Robbins (1942) have shown hat resistance of the seedling to infection is correlated with the difficulty of puncturing the cell-wall, this in turn being largely due to the amount of secondary thickening and lignification. Damping-off fungi are therefore mainly restricted in their attack to young tissues such as root-tips and outright killing of the host will only occur where the hypocotyl region is till succulent and unlignified. Environmental conditions favouring the peedy maturation of the seedling tissues (rather than rapid growth, although the two may be linked), such as high light intensity (Tint, 1945; Vaartaja, 1952), are therefore particularly favourable to the survival of the plant.

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The factor which has been most fully investigated is temperatur Leach (1947) has shown that in all the combinations of host and parasit which he investigated, pre-emergence infection was most severe at temperatures relatively less favourable to the host than the pathogen, a measured by a growth rate ratio. His results uphold the concept outline above. There are also many reports showing that high-temperature crop are most susceptible at low temperatures, and vice versa (Arndt, 1943 Tolba & Moubasher, 1956; Wright, 1957). C. Roth (1935) and Wrigh (1957) also measured the growth rate of the pathogen *in vitro* but foun no consistent relation between it and pathogenicity.

That a similar relationship to that described by Leach (1947) fo temperature probably holds in respect to alteration in the incidence o damping-off with soil pH has been suggested by Beach (1946), and i supported by the work of Arrhenius (1923) on beet and by a large numbe of reports showing that conifers, with a low pH optimum, are least attacke in acid soils. This hypothesis, however, has never been adequately teste and the present paper reports an investigation into the influence of soil p on the host, the pathogen and the disease.

Pythium spp. have been shown to grow over a wide pH range with excellent growth from pH *c.* 4·5–7·0 (C. Roth, 1935; L. F. Roth & Riker, 1943 Carrera, 1951). Studies in the physiology of parasitism of *Pythium*, wit especial reference to the production and activity of pectolytic enzymes have been made by Chona (1932), Ashour (1954) and Gupta (1956). All have shown that the greatest activity occurs in alkaline solutions although there the rate of growth is decreased.

MATERIALS AND METHODS

As hosts, *Picea sitchensis* and *Pinus contorta* were chosen as conifers with known low pH optima, *P. halepensis* as a conifer with a presumed high pH optimum—it is largely restricted to limestone country—*Beta vulgaris* as a plant with known high pH optimum and *Brassica campestris* as a plant with wide pH tolerance. As a parasite, a strain of *Pythium ultimum* Trow of known high virulence was used.

The attempt was made to obtain conditions as near as possible to those in the field, with soils comparable chemically and physically, except in so far as affected by pH, and with a balanced microflora natural to each pH. The experimental soil was therefore made up in the following way from three natural soils which had been shown by previous tests to be relatively free from damping-off fungi.

The main soil used was from Kennington Three forest nursery (Oxford) with pH 5·5. To this was added about one-fifteenth by weight of both Wareham forest nursery (Dorset, pH 4·0) and Rockefeller field (Cambridge, pH 8·0) soils. The reaction of the well-mixed soil was then immediately adjusted with either calcium hydroxide or sulphuric acid. The pH adjustments were made on 8 March 1955 and the soil was then frequently turned and watered till by 28 April steady pH values had been reached. By this means it was hoped to obtain comparatively natural soil populations at each pH, for the small quantities of both acid and alkaline ils would provide a nucleus of those micro-organisms normally present such a pH but absent in the original Kennington Three soil.

On 28 April, the experiment was set up and the soils were placed in 8’ size pots, five pots at each of the nine pH values being allowed for ach plant species. At each pH, three pots were inoculated by mixing 5 g. 3 % cornmeal sand culture of *Pythium ultimum* (grown for 7 days at 2·5° C.) with the top 3 cm. soil, and sixty-four seeds were then sown at ·5 in. intervals and covered with 5 mm. sterile quartz sand. Two pots t each pH were similarly treated but without inoculation. The experiment as conducted in a cool glasshouse and counts of living and dead seedlings ere made every 2 days, dead seedlings being removed, until 22 May for *eta* and *Brassica*, and until 9 September for the conifers, on which dates e plants were harvested.

The accurate measurement of rates of growth of fungi through natural oil is beset by many difficulties. Measurement of growth by inoculation f *Pythium* at one end of a soil recolonization tube (Evans, 1954) followed y sampling the soil at intervals of time along its length, was precluded y the very irregular rates thus obtained and by the fact that the natural oils had a small *Pythium* population. Similarly, measurements based on he rate of spread of disease from a central inoculum through a test crop re insufficiently consistent and accurate. It was therefore reluctantly lecided to investigate the pH relations of the parasite in pure culture on gar.

Experiments showed that a suitable medium consisted of soil extract +0·5 % glucose in 3 % agar, the soil extract being obtained by shaking qual weights of air-dry soil and distilled water, the mixture then being llowed to stand overnight, filtered and autoclaved after addition of the lucose and agar. After adjustment of pH with either N/10 HCl or N/10 NaOH, 15 ml. of medium was poured into growth tubes (Ryan, Beadle & Tatum, 1943), there being four replicates at each of the ten reactions. Each tube was then inoculated with a 4 mm. disk, cut with a sterile no. 1 cork borer from a young colony of the fungus on potato-dextrose agar, and placed at 25° C. Growth along the tubes was measured each day. Using this method with a fast-growing fungus, buffer solutions were unnecessary, for the mycelium constantly grew forwards on to unaltered medium. The low level of carbohydrate and nitrogen in this particular medium was also helpful in maintaining uniform conditions. Measurements of the pH adjacent to the leading edge of the colony after 5 days' growth revealed only small changes.

RESULTS

Pinus halepensis grew well at all pH levels, but the experiment with this species failed owing to the fact that very little damping-off occurred, presumably due to there being insufficient inoculum to cause disease, although the inoculum level was satisfactory for the other test species. *P. halepensis* is not considered further.

The results of the other experiments are presented below, mainly in tabular form. For *Beta* and *Brassica*, the damping-off figure is the *percentage total damping-off* expressed as

$$\frac{\text{Difference between mean numbers of seedlings alive in control and inoculated pots}}{\text{Mean number of seedlings in control pots}} \times 100.$$

The weight of the seedlings is the average fresh weight of shoots and leaves of the seedlings in the control pots.

For the conifers, variability in germination has necessitated the expression of damping-off as a *post-emergent loss*, given as

$$\frac{\text{Number of dead seedlings}}{\text{Number of emerged seedlings}} \times 100.$$

The fresh-weight figures were derived as for *Beta*. Unfortunately, therefore, the measure of damping-off for the two groups differs but the discrepancy between them is reduced as most loss in the conifers appeared to be post-emergent, unlike that in *Beta* and *Brassica*.

The pathogen/host growth ratio is derived from

$$\frac{\text{Growth rate of } \textit{Pythium} \text{ (mm./day)}}{\text{Mean fresh weight of shoot of uninoculated seedlings (mg.)}} \times 100.$$

The *Pythium* growth rate has been read from a graph (Fig. 1).

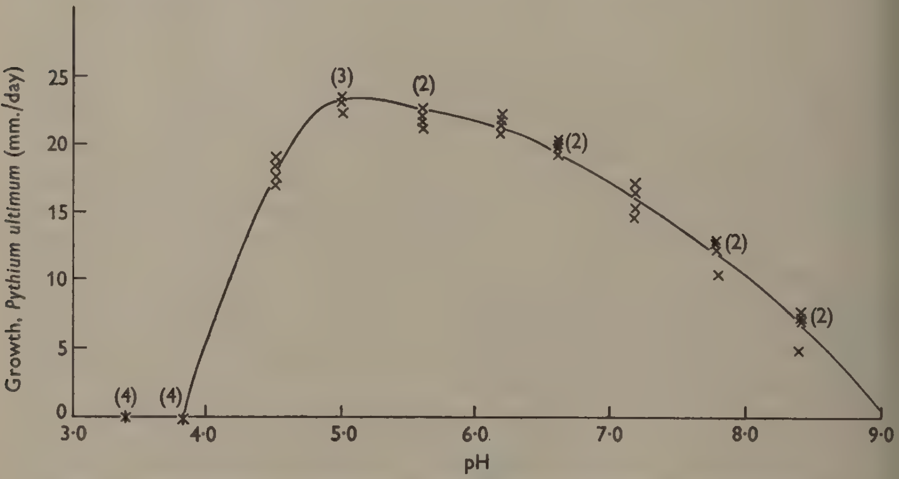

Fig. 1. Relation between pH of the medium and growth rate of *Pythium ultimum*.

Effect of pH *of culture medium on fungal growth*

The relationship between pH of the culture medium and growth rate of *P. ultimum* is shown in the graph (Fig. 1). The maximum, optimum and minimum pH values for growth are shown to be 9·0, 5·0 and 3·8.

Table 1. *Effect of* pH *on damping-off and growth of* Pinus contorta

pH	Mean fresh wt. of uninoculated seedlings in (*a*) and (*b*), control pots (mg.)	Percentage loss through damping-off in inoculated pots				Pathogen/host growth ratio
		(*c*)	(*d*)	(*e*)	Mean*	
3·5	108	0	0	0	0	0
4·2	161	2·0	5·1	0	2·4	0·062
4·8	167	3·6	0	0	1·2	0·132
5·2	148	2·2	19·1	2·6	8·0	0·159
6·1	131	14·3	33·3	12·5	20·0	0·164
6·6	104	14·3	8·3	35·3	19·3	0·188
7·3	84	18·4	40·7	13·3	24·1	0·178
7·6	62	17·9	23·3	39·3	26·8	0·218
8·0	81	44·4	40·9	55·6	47·0	0·123

* The mean value is not used in subsequent calculations.

Table 2. *Effect of* pH *on damping-off and growth of* Picea sitchensis

pH*	Mean fresh wt. of uninoculated seedlings in (*a*) and (*b*), control pots (mg.)	Percentage loss through damping-off in inoculated pots				Pathogen/host growth ratio
		(*c*)	(*d*)	(*e*)	Mean†	
3·5	121	0	0	4·4	1·5	0
4·1	143	25·0	4·4	16·7	15·4	0·052
4·8	102	4·8	22·5	12·5	16·6	0·216
5·2	135	24·2	15·6	60·0	33·3	0·174
6·6	125	39·5	13·2	28·6	27·1	0·156
7·3	142	60·0	20·0	39·0	39·7	0·106
7·6	100	9·1	83·3	32·0	41·5	0·135
8·0	44	16·1	26·9	43·8	28·9	0·227

* Owing to an accident, the pH 6·0 series was lost.
† The mean value is not used in subsequent calculations.

Table 3. *Effect of* pH *on damping-off and growth of* Beta vulgaris

pH	Mean fresh wt. of uninoculated seedlings in (*a*) and (*b*), control pots (mg.)	Percentage loss through damping-off in inoculated pots				Pathogen/host growth ratio
		(*c*)	(*d*)	(*e*)	Mean*	
3·5	8	97·3	89·0	91·8	92·7	0
4·0	14	92·5	66·4	60·8	73·2	0·357
4·8	41	35·7	76·2	64·3	58·7	0·537
5·2	47	55·1	60·2	85·7	67·0	0·500
6·0	111	56·2	61·9	14·3	44·1	0·198
6·5	90	33·9	35·7	65·6	45·1	0·222
7·2	48	29·3	37·9	63·8	43·7	0·333
7·6	59	54·2	47·9	45·8	49·3	0·229
8·0	31	34·7	46·5	66·7	49·3	0·323

* The mean value is not used in subsequent calculations.

Effect of soil pH *on host growth*

In general, the species reacted as anticipated, the conifers growing best in acid, *Beta vulgaris* in near-neutral soils and *Brassica campestris* revealing no marked preference over a wide pH range, except for a diminution in

Table 4. *Effect of* pH *on damping-off and growth of* Brassica campestris

pH	Mean fresh wt. of uninoculated seedlings in (*a*) and (*b*), control pots (mg.)	Percentage loss through damping-off in inoculated pots				Pathogen/host growth ratio
		(*c*)	(*d*)	(*e*)	Mean*	
3·5	3·4	78·4	40·5	78·3	65·7	0
4·0	23·4	54·4	57·0	29·1	46·8	0·214
4·8	69·0	−3·0	43·3	30·0	23·4	0·319
5·2	106·0	−30·0	50·0	15·0	11·7	0·222
6·0	70·0	64·9	54·0	71·1	60·0	0·314
6·5	96·0	6·1	2·0	51·0	19·7	0·208
7·2	98·0	25·8	48·4	22·6	32·3	0·163
7·6	50·0	48·7	48·7	59·0	52·1	0·270
8·0	86·0	35·4	16·9	26·2	26·2	0·116

* The mean value is not used in subsequent calculations.

growth at very low pH values. Testing for a linear regression, only *Pinus contorta* yielded a correlation coefficient significant at the 5 % level and even here a more complex relationship is strongly indicated.

P. contorta. $Y = 116 - 17\cdot4\ (x - 5\cdot9)$. S.E. $= 27\cdot1$; $r = -0\cdot738$; D.F. $= 7$. Probability $< 5\ \%$. ($Y =$ wt., $x =$ pH.)

Effect of soil pH *on damping-off*

Only *Brassica campestris* failed to give a significant correlation between soil pH and damping-off. For the other three species, the results are in conformity with field experience, loss increasing with pH for the conifers and decreasing for *Beta vulgaris*.

Pinus contorta. $Y = 16\cdot5 + 9\cdot0\ (x - 5\cdot9)$. S.E. $= 9\cdot9$; $r = 0\cdot644$; D.F. $= 25$. Probability $< 0\cdot1\ \%$.

Picea sitchensis. $Y = 25\cdot0 + 7\cdot2\ (x - 5\cdot9)$. S.E. $= 17\cdot5$; $r = 0\cdot569$; D.F. $= 22$. Probability $< 1\ \%$.

Beta vulgaris. $Y = 58\cdot0 - 8\cdot8\ (x - 5\cdot9)$. S.E. $= 13\cdot8$; $r = -0\cdot608$; D.F. $= 25$. Probability $< 0\cdot1\ \%$. ($Y = \%$ loss, $x =$ pH.)

Effect of growth rate of host on damping-off

Only with *Picea sitchensis* was the correlation not significant. With the other three species there was a strong negative correlation between the weight of uninoculated seedlings and loss from damping-off in inoculated seedlings.

Pinus contorta. $Y = 16\cdot5 - 0\cdot43\ (x - 116)$. S.E. $= 6\cdot9$; $r = -0\cdot916$; D.F. $= 25$. Probability $< 0\cdot1\ \%$.

Beta vulgaris. $Y = 58\cdot0 - 0\cdot37\ (x - 50)$. S.E. $= 19\cdot3$; $r = -0\cdot531$; D.F. $= 25$. Probability $< 1\ \%$.

Brassica campestris. $Y = 38\cdot7 - 0\cdot48\ (x - 67)$. S.E. $= 23\cdot6$; $r = -0\cdot575$; D.F. $= 25$. Probability $< 1\ \%$. ($Y = \%$ loss, $x =$ fresh wt.)

Effect of growth rate of pathogen on damping-off

In no case was there a significant correlation between damping-off and rate of growth of *Pythium* (taken from the graph).

Effect of pathogen/host growth rate ratio on damping-off

Only in the case of *Pinus contorta* did this relationship give a significant correlation.

P. contorta. $Y = 16{\cdot}5 + 204\ (x - 0{\cdot}136)$. S.E. $= 10{\cdot}5$; $r = 0{\cdot}792$; D.F. $= 25$. Probability $< 0{\cdot}1\ \%$. ($Y = \%$ loss, $x =$ growth rate ratio.)

DISCUSSION

From the analysis of results presented above, it is clear that of the factors studied, the main one affecting changes in incidence of damping-off with change in soil pH is the vigour of the host, as expressed in its growth rate during the susceptible period. Three of the four host species show a strong negative correlation between incidence of disease and growth rate. Conversely, the rate of growth of the pathogen apears to be of little importance, for no species reveals a significant correlation between incidence of disease and the pathogen growth rate on an agar medium. Perhaps a better correlation would be obtained if the growth rate were measured in soil, but the result is not unexpected in view of the discrepancy between growth rate and pectolytic enzyme production in *Pythium* (Chona, 1932; Ashour, 1954; Gupta, 1956). One species only, *Pinus contorta*, shows a significant correlation between damping-off and the pathogen/host growth rate ratio, and the strength of this association is largely due to the strength of the corresponding inverse one between disease and host growth.

The situation with regard to damping-off and soil pH is therefore different from the corresponding relation between pre-emergence damping-off and temperature described by Leach (1947), where the growth rates of host and pathogen are both of importance. It is, however, similar to that described for temperature by C. Roth (1935) and Wright (1957) in indicating the apparent unimportance of pathogen growth rate and the great importance of host vigour.

Although these results indicate that, in the pH range investigated, alteration in pathogen growth rate is unimportant in relation to disease incidence, this is not to be taken as a contradiction of Garrett's (1956) emphasis on the importance of the pathogen growth rate in damping-off diseases. First, the dispersion of inoculum by thorough admixture with the soil would have reduced to a minimum the distances between seedlings and the damping-off fungus, so that any possible effect of soil conditions upon fungus spread through the soil would thereby have been minimized. Secondly, throughout nearly the whole range pH 4·0–8·0 the growth rate of the fungus was very high and over half-maximal. These considerations probably explain why the main effect of soil pH on damping-off appears to have been mediated by the variation in seedling susceptibility induced by this factor.

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CROOK ROOT OF WATERCRESS

III. THE CAUSAL ORGANISM *SPONGOSPORA SUBTERRANEA* (WALLR.) LAGERH. F.SP. *NASTURTII* F.SP.NOV.

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(With Plate 27 and 4 Text-figures)

A description is given of the morphology of the fungus responsible for the crook root disease of watercress. The host–parasite relations of the disease are briefly discussed and cross-pathogenicity studies are described. The fungus is identified as a hitherto undescribed forma specialis of *Spongospora subterranea* (Wallr.) Lagerh., differing in pathogenicity from the f. sp. causing powdery scab of potato.

INTRODUCTION

Crook root disease of watercress (*Nasturtium officinale* R.Br. and *N. officinale* × *N. microphyllum* Boenn. ex Rchb.) was first discovered in Britain in 1948 by officers of the National Agricultural Advisory Service. By 1950 it had been reported from all the principal watercress growing regions and had become a serious threat to the industry (Howard & Lyon, 1950; Spencer, 1951). What appears to be the same disease has recently been found in Belgium (Parmentier, 1956).

The initial research on the disease was done by Spencer & Glasscock (1953), who described the symptoms and found that the cause was a water-borne fungus. The fungus infected the watercress roots causing them to become swollen, distorted and crooked. Infected plants lost vigour, became stunted and often eventually died. Zoosporangia and spore balls were found in the cells of the roots and the fungus was tentatively identified as a species of *Spongospora* (Howard & Lyon, 1950).

My investigation started in 1952 in continuation of the work of Spencer. Studies on the factors affecting the severity and distribution of the disease and on methods of control have been published elsewhere (Tomlinson, 1958*a*, *b*). The present work describes the morphology and pathogenicity of the disease organism which I have identified as a forma specialis of *S. subterranea* (Wallr.) Lagerh.

HOST–PARASITE RELATIONS

During the field studies from 1952 onwards, the following symptoms of the disease and stages of the fungus within the diseased roots were observed.

From October to April, the crop in an affected bed gradually declines. The plants near the water outlet suffer first and the effects of the disease become progressively more obvious from the bottom to the top of the bed, until, finally, only a few yards of healthy plants remain around the water inlet. The most obvious symptom is a general decline in plant vigour and a chlorosis or blueing of the leaves. Associated with these aerial symptoms are the characteristic swellings and crooks on the roots which are much reduced in size (Pl. 27, fig. 1). Sections of the diseased roots show that the outer cells are enlarged and contain plasmodia and zoosporangia from which zoospores are released. These swim, or are carried in the water current, to other roots which they infect. They then develop into further plasmodia and zoosporangia, this cycle being repeated every 7–10 days. Experiments on the distribution of the disease in watercress beds have shown that the incidence of root infection is related to the distance of the plants from the water inlet to the bed; a phenomenon associated with the concentration of zoospores in the water (Tomlinson, 1958*a*).

From May to September, crook root infection declines and crops rapidly increase in vigour. Plasmodia in infected roots, though occasionally forming zoosporangia, mostly differentiate into spore balls which are formed in large numbers in the outer cells of the root. Spore balls consist of sponge-like aggregates of spores. Their germination has not been observed but, by analogy with those of *S. subterranea*, they are presumed capable of survival for long periods, eventually germinating to produce zoospores.

Factors affecting the decline of the disease in the summer and the initiation of spore ball production are unknown.

Detailed descriptions of these various stages of the fungus are given below.

MORPHOLOGY

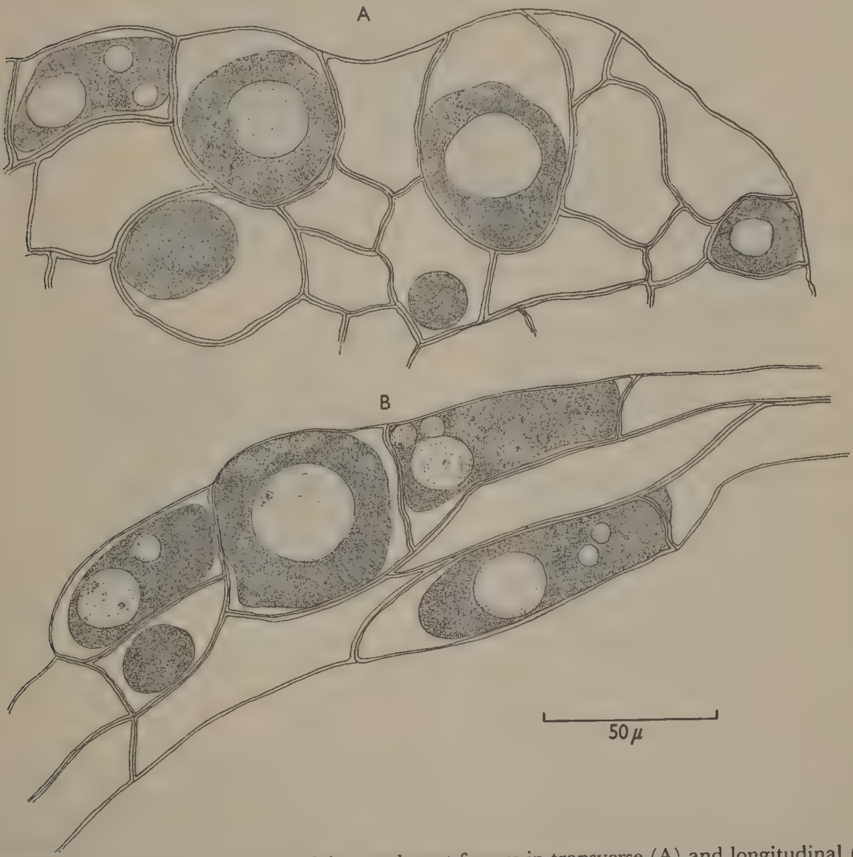
The following description is based on the fungus as found in diseased roots of the brown variety of watercress (*N. officinale* × *N. microphyllum*) collected at Bere Regis, Dorset. Observations on specimens of the fungus obtained from other districts showed the Bere Regis material to be typical. The description of the microscopic characters is based partly on hand sections of fresh material mounted in distilled water, and partly on material sectioned or teased out in lacto-phenol or lacto-phenol with cotton blue.

Plasmodia

Plasmodia develop in the outer cells of the root following their invasion by zoospores. Each plasmodium apparently arises from one zoospore which rounds off in the cell and enlarges considerably, filling almost the entire cell space. Before its differentiation into zoosporangia, each plasmodium contains a large central vacuole and the protoplasm is finely granular and sometimes faintly yellow in colour. The shape and size of the plasmodium is determined by that of the occupied cell. In transverse root sections (Text-fig 1 A) plasmodia are mostly spherical and approximately 50 μ diam., while in longitudinal root sections (Text-fig. 1 B) they appear as elongated structures up to 130 μ in length.

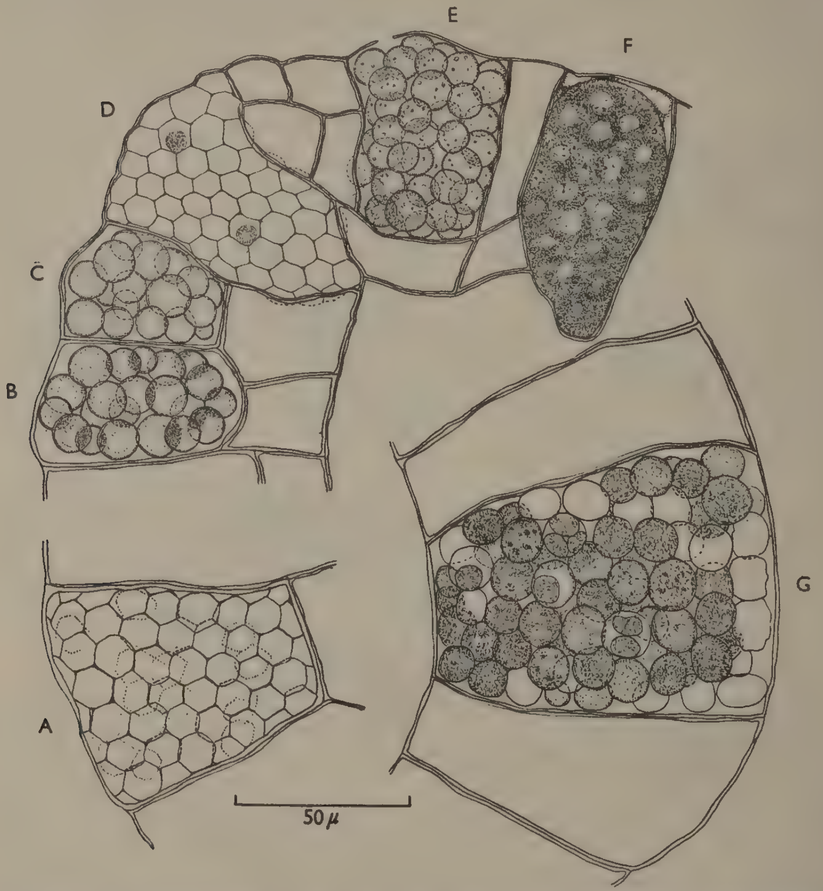
Zoosporangia

As the plasmodium matures, portions of it become condensed and round off into separate zoosporangia. These are spherical with smooth, thin walls (Pl. 27, fig. 2). They are sometimes faintly yellow or orange in colour and 6·0–12·0 μ (average 9·3 μ) diam. (Text-fig. 2).



Text-fig. 1. A and B, plasmodia of the crook root fungus in transverse (A) and longitudinal (B) root sections. The plasmodia are irregular in shape and, when mature, contain a large vacuole.

When mature, each zoosporangium germinates and generally releases four zoospores which escape from the cell into the surrounding water. Though zoosporangia were observed for long periods in root sections mounted in water, their germination was observed only rarely. In such instances the release of zoospores from the cell was preceded by much agitation and vibration of the zoosporangia within it. It appeared that the zoospores were released first from the zoosporangia and then through a small hole in the wall of the parasitized cell. On rare occasions a zoospore was observed for a fleeting moment to be trapped in the hole of the cell wall before wriggling free into the surrounding water. Germination of the zoosporangia within the cell occurred successively and at random, and was usually completed in 30–60 min.

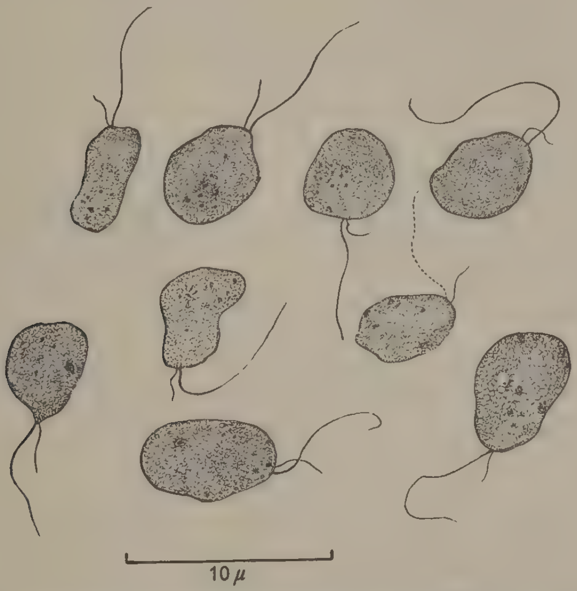


Text-fig. 2. A–G, zoosporangia of the crook root fungus in varying stages of development in transverse root sections. Development of zoosporangia occurs following the differentiation of a plasmodium (F) into separate units which round off into zoosporangial clusters (B, C, E and G); E shows a hole in the cell-wall through which zoospores escape at the time of germination; G, a zoosporangial cluster during germination; A and D, germinated zoosporangial clusters.

The empty zoosporangia became hexagonal in shape. This may have resulted from the disappearance of internal cell pressure and the contraction of the cell wall assisted, possibly, by the outward wall pressure of adjacent turgid cells.

Zoospores

Zoospores were examined swimming in water under a 1·8 mm. obj. After their escape from the zoosporangial cluster they either swam away instantly or remained for a brief period (exhibiting amoeboid movements) on the surface of the parasitized or a nearby cell and then swam away in random directions. Swimming zoospores were generally spherical or pyriform though subject to changes in shape. They were biflagellate and heterokont, the short flagellum measuring about half and the long flagellum about three times the diameter of the zoospore (Text-fig. 3). After 1–2 hr. the zoospores ceased swimming and became spherical. The long flagellum undulated for some time afterwards. In such condition

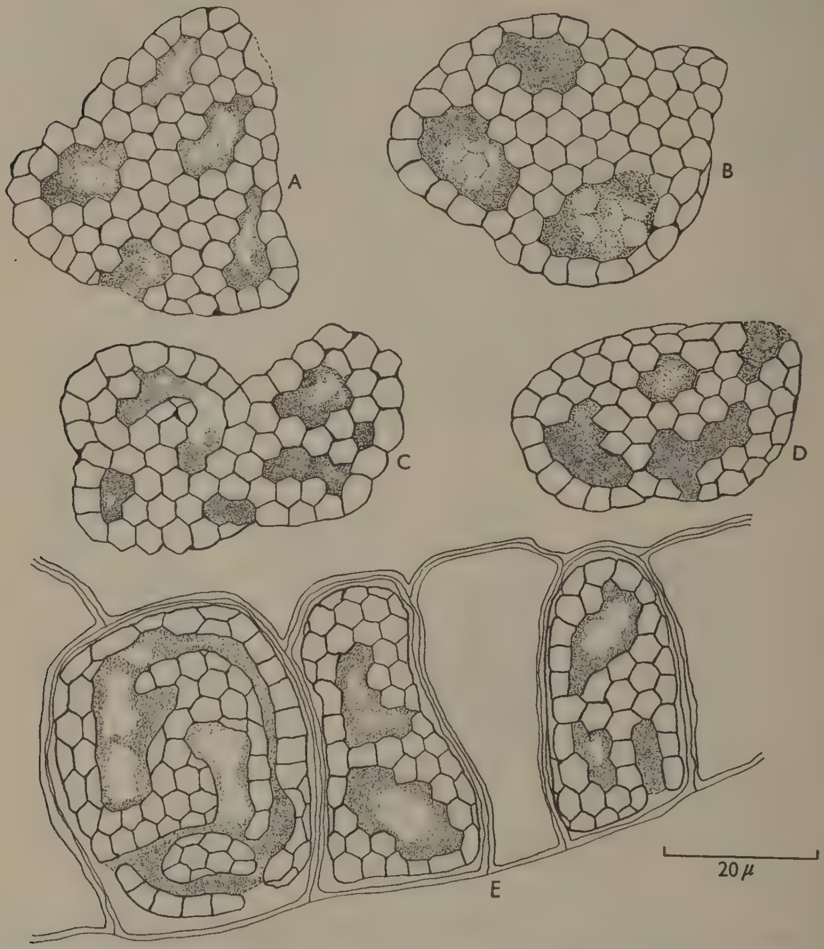


Text-fig. 3. Biflagellate, heterokont swimming zoospores of the crook root fungus immediately after their escape from the host cell.

zoospores measured 2·4–6·0 μ (av. 4·6 μ) diam. The protoplasmic contents of the zoospores were hyaline but usually contained several large refractive granules and vacuoles. Fusion of zoospores and the occurrence of zoospores with four and six flagella, as described for *S. subterranea* (Kole, 1954), were not observed with the zoospores of the crook root fungus.

Spore balls

A spore ball is formed by the differentiation of a plasmodium into a large number of resting spores arranged to form a hollow, irregularly channelled, spongy structure. The spores in the spore ball are hexagonal or polygonal in shape, 3·3–4·4 μ (av. 3·9 μ) diam., with thin walls which are yellow at first but later generally become brown in colour (Pl. 27, figs. 3, 4). The spore balls are irregular in shape and tend to assume the shape of the occupied cell (Text-fig. 4).



Text-fig. 4. A–D, spore balls of the crook root fungus consisting of hexagonal, smooth-walled resting spores arranged in irregularly channelled hollow balls; E, spore balls in the outer cells of the root.

PATHOGENICITY

Roots of the following species of plants growing as weeds in commercial beds of watercress (and, therefore, exposed to continual zoospore infection) were found to be healthy: *Myriophyllum spicatum*, *Ranunculus aquatilis*, *Callitriche* spp., *Lemna* spp., *Apium nodiflorum*, *Veronica beccabunga*, *V. anagallis-aquatica*, *Mentha aquatica*, *Equisetum fluviatile*, *Glyceria aquatica*, *Berula erecta*.

Cross-inoculation tests with the crook root fungus and with *S. subterranea* were made to healthy rooted watercress cuttings and healthy rooted tomato seedlings (cv. Harbinger). The tests were made in a way similar to that used for standard infection tests in other studies on crook root (Tomlinson, 1958*a*). To provide inoculum of the crook root fungus, infected watercress cuttings were grown in boiling tubes containing 80 ml. of autoclaved river water, which favoured high infection (Tomlinson, 1958*a*), there being one cutting per tube. In each tube was also placed either a healthy watercress cutting or a healthy tomato seedling. There were five tubes each containing two watercress plants, and five tubes each with one watercress and one tomato plant.

Within 10 days all the healthy watercress cuttings had become infected by zoospores liberated from the infected cuttings and bore crooked roots. The roots of all the tomato plants, however, were still healthy after 21 days.

Inoculations with *S. subterranea* were made by growing a tomato seedling and a healthy watercress cutting in the same tube with 80 ml. of water to which was added 0·15 g. of a suspension of spore balls of the fungus. These were obtained by scraping the powdery scab lesions from diseased potato tubers, the dried scrapings being ground to a powder in a mortar. There were 5 such infection tubes.

After 20–30 days, numerous biflagellate, heterokont zoospores were visible in the root hairs and epidermal cells of the tips of the tomato roots in all the tubes, thus demonstrating infection. Such infections, however, did not occur on the roots of the watercress cuttings.

Similar cross-inoculations with the crook root fungus and *S. subterranea* were made to rooted potato stems but the tests were unsuccessful because of the rapid bacterial breakdown of the potato stems.

The results of these tests show that the crook root fungus differs from *S. subterranea* in pathogenicity to watercress and tomato.

IDENTITY

Using Karling's (1942) key, the crook root fungus can be identified as a species of *Spongospora* because of the aggregation of the resting spores into irregularly channelled, sponge-like spore balls. According to Karling the genus comprises two species, *S. subterranea* and *S. campanulae* (Ferdinandsen & Winge) Cook. *S. campanulae* is distinguishable from the crook root fungus by its larger and echinulate-walled resting spores, smaller spore balls and apparent lack of zoosporangia. The resting spores and spore balls of *S. subterranea* from potato were examined and were indistinguishable from the spore balls of the crook root fungus. In Table 1, the dimensions of various structures of the crook root fungus are compared with the dimensions of similar structures of *S. subterranea* as given by Karling. The zoospores, spore balls and resting spores of the two fungi were of similar sizes.

Table 1. *Dimensions (in μ) of the crook root fungus and* Spongospora subterranea

	Plasmodia	Zoosporangia	Zoospores	Spore balls	Resting spores
Crook root fungus	10–130	6·0–12·0	2·4–6·0	18–82	3·3–4·4
S. subterranea	approx. 70	Not given	2·5–3·5	19–85	3·5–4·5

The dimensions of the plasmodia of the crook root fungus were variable, but in transverse root sections, as previously described, they were mostly about 50 μ diam., and were thus of approximately the same size as the plasmodia of *S. subterranea*.

In view of the similarities in sizes between the two fungi and the differences in pathogenicity described previously, I propose to name the crook root fungus a forma specialis of *S. subterranea*.

Spongospora subterranea (Wallr.) Lagerh. f.sp. **nasturtii** f. sp.nov.
(Pl. 27, Text-figs. 1–4)

Varians e forma parasitica *Nasturtium officinale* R.Br. et *N. officinale* R.Br. × *N. microphyllum* Boenn. ex Rchb. radices adunca et magna productus est. Typus: I.M.I. 74293.

Differs from the type in parasitizing *Nasturtium officinale* R.Br. and *N. officinale* R.Br. × *N. microphyllum* Boenn. ex Rchb. causing root distortion and swelling. Type collection on *N. officinale* × *N. microphyllum*, Bere Regis, Dorset, May 1954, coll. J. A. Tomlinson.

The above proposal automatically creates a forma specialis based on the type. Thus, the potato powdery scab fungus becomes *S. subterranea* f. sp. *subterranea*.

My thanks are due to Dr J. Colhoun, Dr A. E. W. Boyd and Dr Elizabeth Gray who provided me with material of *S. subterranea*, and to Miss J. Kullman for the photographs.

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EXPLANATION OF PLATE 27

Fig. 1. Left: healthy watercress plant; right: watercress plant affected by the crook root disease.

Fig. 2. Section of a watercress root showing zoosporangia in two of the outer cells of the root. Some of the zoosporangia have germinated and are empty.

Fig. 3. Part of a watercress root containing spore balls after teasing out in lacto-phenol with cotton blue.

Fig. 4. An individual spore ball, from a teased-out infected root, showing the irregularly channelled hollow structure.

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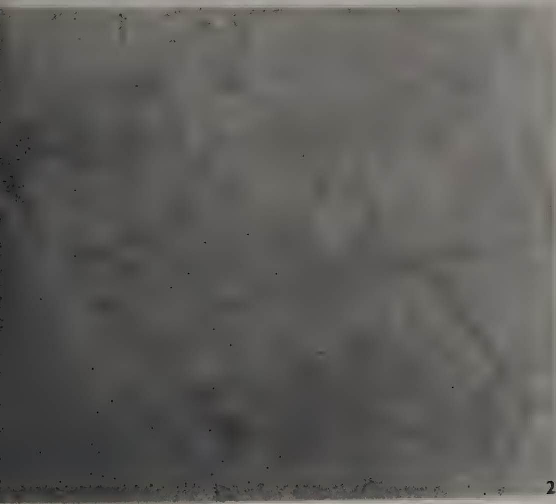

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(*Facing p.* 498)

Trans. Brit. mycol. Soc. **41** (4), 499–500 (1958).

GLIOMASTIX GUTTULIFORMIS SP.NOV.

By JULIET C. BROWN

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AND W. B. KENDRICK*

Botany Department, University of Liverpool

(With Plate 28 and 1 Text-figure)

Gliomastix guttuliformis sp.nov. is described and illustrated, and briefly compared with *G. convoluta* (Harz) Mason.

Gliomastix guttuliformis sp.nov. (Pl. 28, Text-fig. 1)

Coloniae in agaro 'malt' dicto lente crescentes; superne primo hyalinae, deinde margino excepto propter massas conidiales nigrescentes; inferne fulvo-brunneae. *Hyphae* hyalinae, septatae, ramosae, singulatim reptantes, in funiculos floccosos aerios saepe assurgentes. *Conidiophora* ex hyphis reptantibus vel ex funiculosis aeriosis ad paris angulos oriunda, plerumque simplicia, raro versus basin ramosa, subulata, septo subbasali praedita, recta vel curvata, pro parte majore glabra et hyalina, apicem versus tamen aliquando sub-aspera et obscure colorata, 22–52 μ longa, basi 1·6–2·8 μ, subapice 0·8–1·4 μ lata, apice plus minusve infundibulariforme, in discum marginalem 1·0–1·8 μ latum terminata. *Conidia* endogena, guttuliformia, basi truncata, unicellularia, levia, viridinigra, 2·8–4·2 × 2·0–2·8 μ, ex apice conidiophori in capitulum mucosum successive extrusa, una cum illis ex conidiophoris adjacentibus in massam communem saepe coalescentia. Habitat in solo arenoso dunorum Bamburgh, Northumbria, Anglia, atque in foliis putridis *Pini sylvestris* L., Delamere, Cheshire, Anglia. Holotypus in Herb. I.M.I. No. 61279.

Colonies on 2 % malt-extract agar spreading slowly, attaining a diameter of 2 cm. in four weeks at room temperature (Pl. 28, fig. 1). At first low-lying and hyaline, but later, except at the margin, becoming green-black with conidia, and often developing radiating feathery aerial ropes of hyphae (Pl. 28, figs. 2, 4), colony reverse yellowish brown.

Conidiophores typically simple, rarely branched towards the base, with one subbasal septum, straight or curved, smooth and hyaline for most of their length, but slightly roughened and darker toward the apex, 22–52 μ long, 1·6–2·8 μ thick near the base, tapering to 0·8–1·4 μ near the apex; apex more or less infundibuliform, generally with a marginal disk 1·0–1·8 μ diam. The conidiophores are produced either from the surface mycelial mat or along the aerial ropes of hyphae at right angles to their axes. The *conidia* are endogenous, typically drop-shaped, clearly truncate at the narrower basal end, continuous, smooth, green-black, 2·8–4·2 × 2·0–2·8 μ. They are extruded from the apex of the conidiophore in basipetal succession, and accumulate in a slimy head. These masses of conidia often become so large that those of adjacent conidiophores coalesce (Pl. 28, fig. 3).

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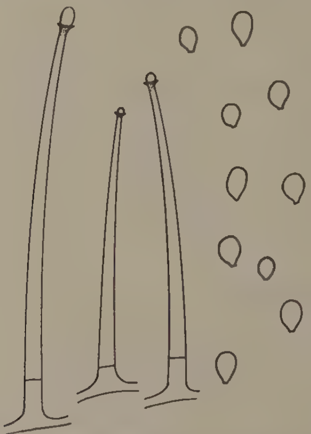
This species resembles *G. convoluta* (Harz) Mason in certain respects, but differs in its more restricted growth in culture, in the presence of a distinct collarette at the apex of the conidiophore, and in the shape of the conidia, which in *G. convuluta* are ovoid to subglobose (Mason, 1941). The conidia of *G. guttuliformis* are considered by the authors to be truly endogenous.



Text-fig. 1. *Gliomastix guttuliformis*. Conidiophores and conidia grown in culture. × 1000.

This species may be placed in section IV of Hughes's recently proposed classification of the Hyphomycetes (Hughes, 1953), as the terminal portion of the conidiophore may be regarded as a phialide, and the conidia as phialospores.

G. guttuliformis has been isolated from the A_1 horizon of fixed sand dunes at Bamburgh, Northumberland (J.C.B., March 1955), and from decaying needles of *Pinus sylvestris* in the A_0 horizon of a podzol at Delamere Forest, Cheshire (W.B.K., December 1956).

We would like to thank Dr M. B. Ellis, Commonwealth Mycological Institute, for his invaluable help in the preparation of the manuscript; also Mr E. W. Mason, Commonwealth Mycological Institute for advice, and Dr V. H. Heywood, Botany Department, University of Liverpool, for assistance with the Latin description.

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EXPLANATION OF PLATE 28

Gliomastix guttuliformis sp.nov.

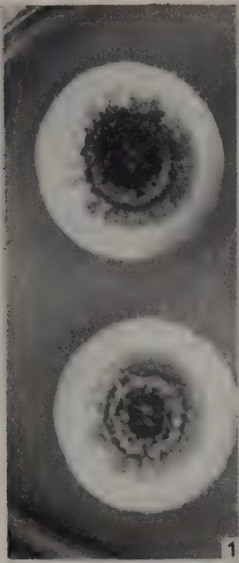
Fig. 1. 4-week-old colonies on 2% malt-extract agar.

Fig. 2. 6-week-old colony on 2% malt-extract agar, showing radiating aerial ropes of hyphae. × 2.

Fig. 3. Margin of 4-week-old colony on 2% malt-extract agar, showing coalescence of adjacent conidial masses. × 80.

Fig. 4. Aerial ropes of hyphae bearing conidiophores. × 100.

(*Accepted for publication* 24 *February* 1958)



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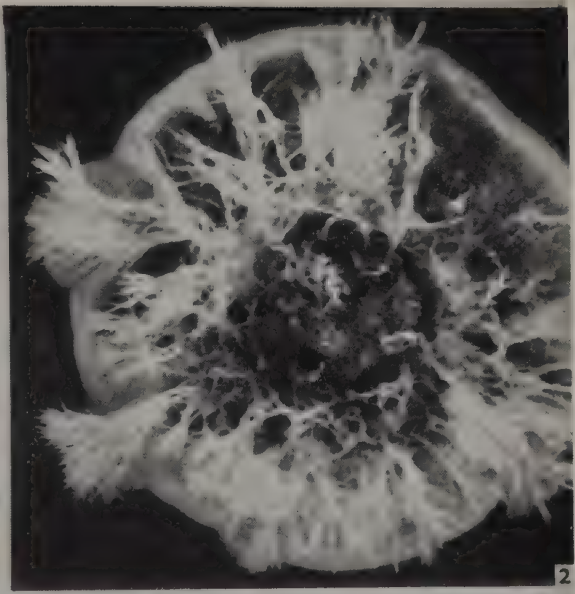

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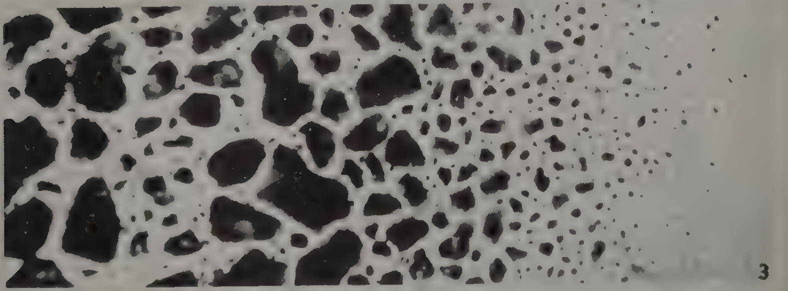

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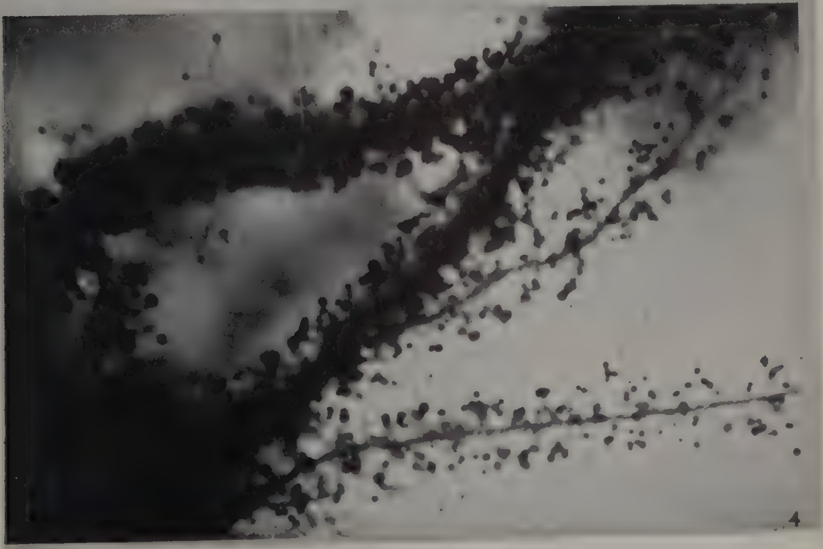

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Trans. Brit. mycol. Soc. **41** (4), 501–504 (1958).

EMERICELLA NIDULANS (EIDAM) VUILL. VAR. *AURANTIOBRUNNEA* VAR.NOV. AND ITS *ASPERGILLUS* STATE

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(With Plate 29)

A strain of *Aspergillus* from Australia with ascospores identical with those of *A. nidulans* but with the radiate conidial head of *A. versicolor* is described as a new variety of *Emericella nidulans*.

Fennell & Raper (1955), in a paper which they state is to be considered in some measure as a supplement to Thom & Raper (1945), added further species and varieties from new strains submitted to them for identification. Four of these belonged to the *Aspergillus nidulans* group, and a fifth, *A. silvaticus* (strain NRRL 2398 from the Gold Coast, Africa), had characters of both the *A. nidulans* and *A. versicolor* groups. Fennell and Raper remarked that they hesitated to place the new species in either group until a general revision of intrageneric relationships and re-evaluation of group characteristics had been undertaken.

A strain of *Aspergillus* (D.S.L. 48) isolated in these laboratories may add fresh light to the problem of assigning *A. silvaticus* to one or other group. The culture had been kept for some years; it was re-examined in detail in 1956, and on Czapek–Dox medium consisted of a dense layer of hülle cells covering perithecia, the conidial heads being relatively few and marginal. Colour was cream or buff and quite unlike the dark green of the surface of *A. nidulans*, while the reverse was golden-brown rather than purplish red, though the latter colour developed slowly when the growing period was over. Although the ascospores had the pleated equatorial crests with sinuous margin of *A. nidulans*, the conidial heads were typically radiate to nearly globose suggestive of *A. sydowi* (Bain. & Sart.) Thom & Church of the *A. versicolor* group and similar to the heads described for *A. silvaticus*. Strain D.S.L. 48 could thus be an ascosporic member of the species *A. silvaticus*, though the conidial heads, which appeared blue-green under the microscope, were not numerous enough to colour the surface of the colonies. Pending a revision of the groups in question, the possession of ascospores identical with those of *A. nidulans* is held to warrant the placing of the strain as a variety of that species.

Details of the strain are as follows:

Colonies on Czapek-Dox solution agar at 30° C. showed restricted growth attaining 3 cm. diam. in 14 days. They were raised and compact, zonate, and the initial white colour turned to cream and buff in the centre after 4 days, the original velvety texture becoming granular and powdery in the same region. The colonies developed a few shallow radial furrows, with the margin lobed between the furrows, and were somewhat irregular in shape. The growing edge was 2–3 mm. wide and was submerged, its colour being the golden-brown of the basal mycelium. Occasional blue-green conidial heads were found at the margin of the raised portions of the colonies, but these were not numerous enough to make green patches or even tinge the general cream colour. Masses of hülle cells came down to the submarginal zone, and there were developing hülle cells between the heads. Drops of golden-brown exudate, about 1 mm. diam. and very regular in size and distribution, lay in the intermediate zones and the reverse of the colonies was likewise golden-brown. A brown pigment similar to the exudate also diffused into the medium. The bright cream or buff of the surface became paler and was almost white after 8 weeks, and the reverse had darkened to brown by that time and became purple after 12 weeks. Continued cultivation from conidia on this medium produced colonies with a pale blue-green surface colour.

The *conidial heads* were more plentiful on Czapek-Dox agar containing double the normal amount of sucrose. Pigment diffused into this medium profusely, and the change in the colour of the reverse of the colonies to brownish purple was more rapid. Otherwise the appearance was similar to that on normal Czapek-Dox agar.

On Raulin–Thom medium the conidial heads grew well and the colony surface appeared a greyish green. On all media the heads were mostly radiate to nearly globose, with sometimes a few short columnar heads where the heads were crowded; reduced forms were also present. The size varied accordingly, but reached a maximum of 250 μ diam. The *conidiophores* were light brown in colour, up to $8 \times 250\,\mu$, with smooth and rather irregular walls. Vesicles were brown, subglobose, fertile over the greater part of the surface (rarely over slightly more than half where the heads were short columnar), and up to 40 μ diam. The relation of the size of vesicle to over-all dimension of head was probably responsible for the ragged appearance of most of the adult heads. There was no indication that the radiate heads were juvenile and the columnar more mature. Foot cells were small and coloured the same as the conidiophores. Sterigmata were in two series and crowded, the metulae av. $7 \times 3\,\mu$ and the phialides $7 \times 2{\cdot}5\,\mu$, though occasional heads had larger sterigmata. *Conidia* were globose to subglobose, up to $3{\cdot}5\,\mu$ in diameter, pale green in mass, and roughened.

Colonies on malt-extract agar appeared basically as on Czapek's agar, showing drops of exudate but no pigment diffused into the medium. The reverse was a dull orange-brown, turning dull purple-brown rapidly. Perithecial development reached its peak on this medium. The *perithecia* were numerous, ovate to globose and $100–150 \times 60–100\,\mu$. Hülle cells were large, thick-walled and globose, some attaining 25 μ diam., growing in dense masses around the perithecia and on the mycelium between them. There was little sterile mycelium, a cross-section of a colony showing the *A. nidulans* pattern of perithecial arrangement (Thom & Raper, 1945, fig. 42). The hülle cells often obscured the purple-red walls of the perithecia and the ascospores within. *Asci* were round and 8-spored, breaking down quickly to set the ascospores free. *Ascospores* were lenticular, smooth-walled with two equatorial crests, which were pleated and had sinuous and entire margins about 1 μ wide; the spore bodies measured up to $4{\cdot}5 \times 4\,\mu$ the over-all size being $6{\cdot}5 \times 6\,\mu$. The colour of the ascospores was a bright purple-red.

DISCUSSION

D.S.L. 48 thus differs from *A. nidulans* (type strain NRRL no. 187) in its more profuse hülle cells, reduced number of conidial heads, golden-brown reverse during the growing period, lack of macroscopic green in the colour of the surface, and by the radiate arrangement of its sterigmata. Kinship with the type strain is established by the purple-red ascospores with pleated crests and smooth walls. For further evidence of the relation of D.S.L. 48 to the *A. nidulans* group, some of the mycelium was cultivated on Raulin–Thom solution and submitted to the colour reactions described by Howard & Raistrick (1955) for the detection of asperthecin pigment, which these authors found frequently in strains of species of the *A. nidulans* group. Eleven tests described to identify the pigment in the culture solution mycelium gave a positive result for asperthecin, though no attempt was made to isolate the colouring matter in pure form. These tests were considered to be sufficient to establish that asperthecin was present; they did not link the strain with *A. nidulans* as an individual species, for the pigment is common to other ascosporic members of the group.

The radiate arrangement of the sterigmata of the conidial heads in D.S.L. 48 seemed, however, to establish a genuine difference from *A. nidulans* and to link the strain with the *A. versicolor* group. If the classification of the Fungi Imperfecti is based primarily on the type of conidial fructification, as stated for instance by G. Smith (1954), one would expect species with columnar heads to be included in the *A. nidulans* group and those with radiate heads in the *A. versicolor* group, and D.S.L. 48 would occupy the anomalous position of an ascosporic member of the *A. versicolor* group. Stolk & Meyer (1957) place their new species *A. raperi* in this latter group, mainly because it possesses radiate conidial heads and a subglobose vesicle fertile over most of the surface; they state, however, that it cannot be fitted into *Aspergillus* as outlined in Thom & Raper (1945). Fennell & Raper (1955) hesitate to take such definite action with *A. silvaticus*. Should ascosporic strains of these species be found, it is possible that they may conform to the *A. nidulans* pattern as do their existing hülle cells. The recent discovery of an ascosporic strain (NRRL no. 2393) of *A. unguis* (Fennell & Raper, 1955), which had been placed in the *A. nidulans* group with reluctance because non-ascosporic, though its other features conformed with group characters, shows that the perfect states of these fungi are likely to occur. Moreover, Thom & Raper (1945) have placed *A. caespitosus* in the *A. nidulans* group on grounds other than shape of conidial head, and *A. janus* in the *A. versicolor* group, although the adult heads are columnar.

Although similarities in asexual characters frequently give clues to relationships, it is recognized that the elucidation of natural relationships among the Fungi Imperfecti always awaits the discovery and study of sexual stages. We suggest therefore that D.S.L. 48, on the basis of its perithecia, asci and ascospores, should, in accordance with the International Rules of Nomenclature, be known as a variety of *Emericella nidulans* (Benjamin, 1955), even though the conidial head is of the *A. versicolor* pattern, rather than as an ascosporic variety of *A. versicolor*. In an attempt to relate the strain to one or other group, biochemical tests were conducted on the golden-brown pigment to see whether it was sterigmatocystin (Birkinshaw & Hammady, 1957) obtained from a culture (L.S.H.T.M. Cat. no. A262) of *A. versicolor*, or quadrilineatin (Birkinshaw, Chaplen & Lahoz-Oliver, 1957) from *A. quadrilineatus* of the *A. nidulans* group, but it differed from both of these. We therefore suggest that, until group relationships of the Aspergilli be re-evaluated, the name *Emericella nidulans* var. *aurantiobrunnea* would be appropriate for type strain D.S.L. 48 and offer the following description:

Emericella nidulans (Eidam) Vuill. var. **aurantiobrunnea** var.nov. (Pl. 29).

A typo differt reverso aurantio-brunneo; capitibus conidicis radiatim dispositis, plerumque 250 μ in diam.; atque vesiculis fere globosis, plerumque 20 μ in diam.; sterigmatibus biseriatis, confertis, primariis 7 × 3 μ secondariis 7 × 2·5 μ. In culturis e solo, Australia. Typus: Herb. I.M.I. 74897.

Type strain D.S.L. 48 was isolated in 1944 from a canvas respirator haversack in Australia. A sub-culture has been deposited in the culture collection of the Commonwealth Mycological Institute.

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EXPLANATION OF PLATE 29

Emericella nidulans var. *aurantiobrunnea* var.nov.

Figs. 1, 2. Colonies growing on Czapek and malt agars after 10 days. × 2.

Fig. 3. Radiate conidial head showing a subglobose vesicle passing almost imperceptibly into the apex of the conidiophore; sterigmata crowded and in two series. × 850.

Fig. 4. Developing globose hülle cells. × 850.

Fig. 5. Asci containing groups of eight ascospores. × 850.

Fig. 6. Ascospores seen on edge with the equatorial crests and sinuous margins prominent. × 1500.

Fig. 7. Ascospores in side view showing the pleated equatorial crests. × 2000.

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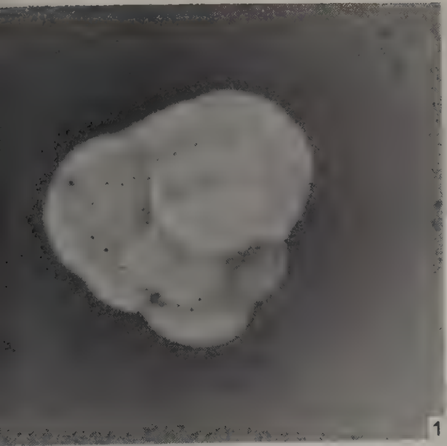

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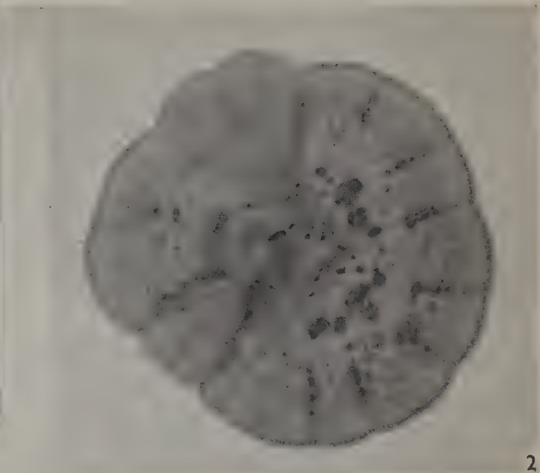

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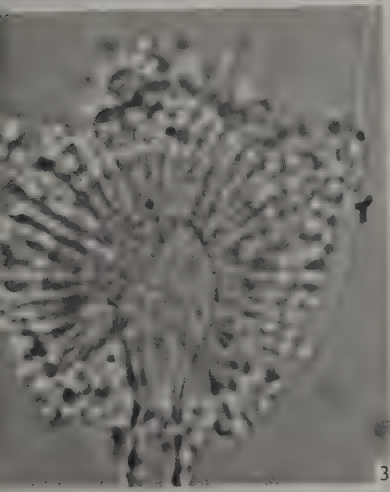

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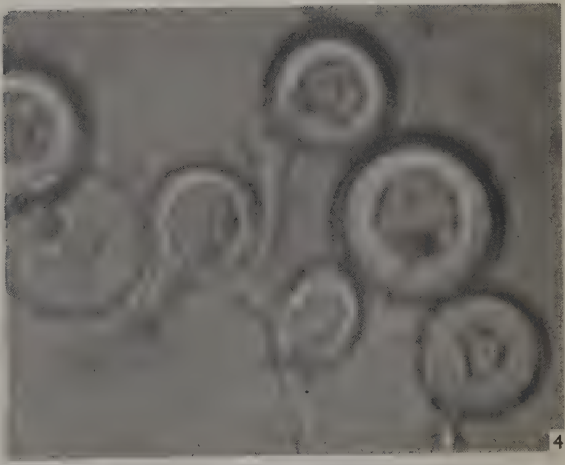

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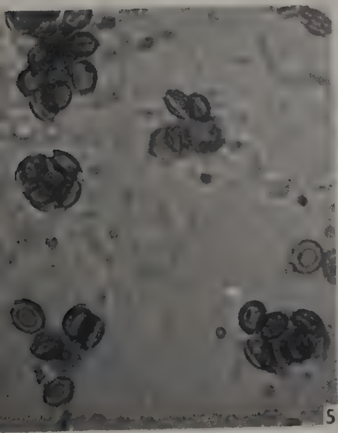

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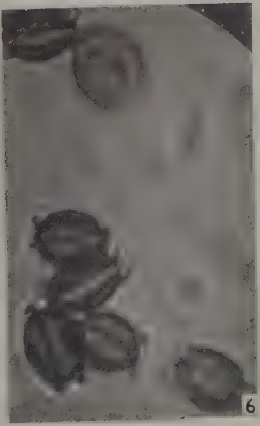

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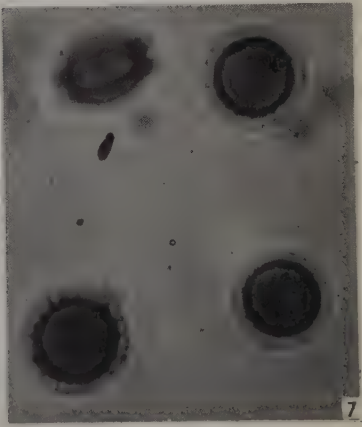

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SOME OBSERVATIONS ON *SEPTORIA GLADIOLI* PASS.

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(With 1 Text-figure)

A survey of herbarium material of the genus *Gladiolus* suggests that *Septoria gladioli* Passerini is endemic on the species of *Gladiolus* native to Europe and was present in Europe before the gladiolus was cultivated on a large scale. Its status in Africa is doubtful. A study of the life history of the fungus, in relation to the gladiolus disease, shows that infection of the leaf bases overlying the corm (and formation of small sclerotia on these leaf bases) is the stage responsible for much of the re-infection of corms each season. Another important stage is the development of primary infections and leaf-to-leaf infection, in plants derived from cormlets and seedlings. Pycnidia and pycnidiospores can only be found on such young plants of cultivars. The fungus is also very persistent in the corm and no treatment in use at present is likely to eradicate it. The fungus in the leaf bases is more easily killed, but more work on fungicides, related to the known life history of the fungus, is required.

INTRODUCTION

Septoria gladioli was first described by Passerini (1874) from the leaves of *Gladiolus segetum* Ker-Gawl. at Parma, Italy. It was again recorded by Allescher (1901) on *G. palustris* Gaud. and *G.* × *gandavensis*, one of the early cultivated hybrids. Ritzema Bos (1906) in Holland noted a corm disease of cultivated gladioli which he later claimed to be *S. gladioli*, though this identification is open to doubt and he may have been describing symptoms of *Sclerotinia gladioli*. Wallace, in an unpublished thesis of 1909 (quoted by Massey, 1916), also noted a corm disease of cultivated gladiolus which was probably caused by *Septoria gladioli* and he called this disease 'hard rot'. Massey (1916) published the first detailed account of the fungus in relation to the gladiolus disease, recording the pycnidial stage for the first time in the United States and showing that both leaf and corm symptoms were caused by the same organism. He also recorded the disease on gladiolus importations from Germany and Holland.

Pape (1926) published a description of the disease and claimed that some cultivars and the species *G. primulinus* Baker were resistant. Drayton (1928) described the disease in Canada, mentioning in his description the presence of minute black spots on the corm scales, which he considered to be incipient pycnidia. The disease was first reported in England by Hodson & Beaumont (1926) and since that time it has been reported frequently. It was noted in France in 1928, in Denmark in 1929 and in Switzerland in 1931.

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In recent years, attention has been concentrated chiefly on field control rather than on the life history of the fungus on which no detailed work seems to have been undertaken since Massey (1916). Moore (1939) published an account of the disease based on a survey of the literature up to that date, and Nelson (1948) has also published an account for the benefit of commercial growers in America.

During the course of a study of gladiolus diseases at Cambridge during 1951–54, *S. gladioli* was investigated in some detail and some of this work is described below.

ORIGIN OF THE DISEASE

A survey of the horticultural literature has shown that species of *Gladiolus* have been cultivated in Europe since the sixteenth century, the first species to be cultivated being *G. segetum* Ker-Gawl. and *G. communis* L., which are native to Europe. Records of cultivation are given in Donn's *Hortus Cantabrigensis* which records the plants that have been grown in the Cambridge Botanic Garden with the dates of their introduction. The first African species were introduced in 1745 and from that date many different species were cultivated, though probably not in great quantities. The first published record of hybridization is that of Herbert in 1822, who recorded the crossing of various African species with each other to produce fertile hybrids. Among the species used were *G. tristis* L., *G. cardinalis* Red., *G. hirsutus* Jacq. and *G. floribundus* Jacq. *G. × colvillei* was produced in 1823 from a cross between *G. tristis* L. and *G. cardinalis* Red. and from this have arisen the early-flowering types, by further hybridization with the African and European species. *G. × gandavensis* was distributed in 1843. It was a cross between African species, though the exact parentage is not certain. From this stock have developed the present-day large-flowered types. The parentage of the modern gladioli is very mixed but its main source is certainly the African species, with possibly a small contribution from the European species.

At first there is no mention of any disease attacking these cultivated hybrids, but Allescher (1901) recorded *S. gladioli* in Portugal on *G. × gandavensis*. Since then, records of the disease have occurred in all areas where the gladiolus is cultivated and all types seem to be attacked.

The leaf-spotting (pycnidial) stage of this fungus is easily recognized on herbarium material and can be identified with reasonable certainty by means of a hand-lens. A survey of herbarium material of the genus *Gladiolus* was therefore undertaken at the Cambridge and Kew Herbaria. At Cambridge, specimens of the related genera *Watsonia* and *Antholyza* were also examined. The frequency of the disease on the specimens and on the various species was noted (see Appendix).

Since all the specimens were wild species collected for botanical rather than for mycological purposes, it was hoped that some indication of the place of origin of the disease might be found. The specimens were roughly divided into African and European species, the former including Madagascar and other islands off the coast of Africa and the latter including

Asia Minor and the Mediterranean coast of North Africa. No gladioli are known to be native in Australasia or America.

At the Kew Herbarium, 450 sheets of European species were examined, comprising sixteen different species. Thirty-seven of these showed leaf spotting caused by *S. gladioli*, in specimens of eight species. At Cambridge, 144 sheets of European gladioli comprising nine species were examined and *S. gladioli* was identified on fourteen of these. Thus, the disease was found on just under 10 % of the specimens examined, a remarkably high value, when one considers that the specimens were not collected to illustrate the disease.

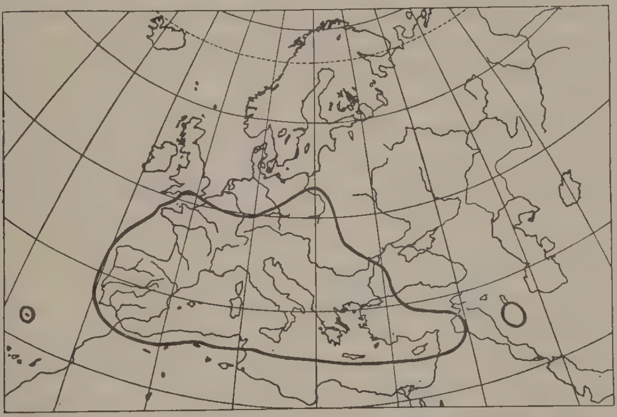

Fig. 1. Distribution of *Septoria gladioli* on wild species of *Gladiolus* in Europe.

A total of 443 sheets of African species was examined at Kew and of these five showed a leaf spotting which resembled that caused by *S. gladioli*. On comparison with known specimens of the the disease, they did not appear identical, but it would have required a more detailed microscopical examination to confirm the identification. At Cambridge, 126 sheets of African species of *Gladiolus* and related genera were examined but none showed any sign of infection.

The geographical positions of the records were plotted and are shown in the accompanying map (Fig. 1). This shows that the disease is widespread in Europe, occurring in all areas where the gladiolus grows wild. It is interesting to note that some of the specimens examined were collected before 1874 when *S. gladioli* was first described, and several were collected in localities where gladioli are not likely to have been cultivated at that date.

This suggests that *S. gladioli* may be endemic on certain species of *Gladiolus* in Europe and that it has spread to other parts of the world and to the cultivars in the last hundred years as the gladiolus has become a popular garden plant. It is possible that the disease is also present on the African species but that the pycnidial stage is not produced on mature plants of flowering size, as happens with some of the cultivated hybrids. This has not been either proved or disproved so far, but plant pathologists have now visited many of the localities where African species of *Gladiolus* grow, and yet I have found no record of *S. gladioli* on wild species in Africa.

THE CYCLE OF INFECTION

The symptoms of the disease caused by *S. gladioli* can best be considered in three phases, leaf infection, infection of young corms, and re-infection of both young and old corms each season.

Leaf infection

Leaf infection is only important on young plants of the cultivated gladiolus, that is, plants in the first two years from seed, or from cormlets. It is rarely, if ever, found on the leaves of plants of flowering size in the cultivars. On some of the wild species, however, leaf infection is found on plants of all ages, as was shown in the Herbarium survey. The importance of the age of the plant does not seem to have been sufficiently emphasized in previous accounts of the disease. Moore (1939) noted that the pycnidial stage is 'rare on the foliage of large flowering varieties' but did not distinguish between fully grown flowering plants and the younger stages of these cultivars. Massey (1916) had noted the distinction, but nevertheless considered that infection of large corms might occur through wash-down of spores from the leaves.

From early July onwards, leaves of young plants can be found with small water-soaked patches (either round or angular), which gradually turn reddish brown, dry up and become pale grey-brown with a dark edge. They vary from about 3 mm. diam. to long streaks or large irregular patches. Streaks are often bounded by a vein. On the patches the small black pycnidia develop, and under moist conditions the spores are extruded from the ripe pycnidia in an orange mass of mucilage. From the presence of this mucilage and from the distribution of lesions later in the season, it is most likely that dispersal of the spores is by rain splashes.

All parts of the leaf may be affected, from the leaf tip to soil level. On examination, two types of infection may be distinguished. The first lesions to be seen in July are primary infections, produced on the leaves of plants either infected in the previous season (in the case of cormlets infection may have been from the mother corm) or infected from debris in the soil after planting. The fungus can survive the storage period on corms infected the previous season. Primary infections are distinguished by the way in which the lesions are distributed on the leaves. The lesions develop progressively, following the natural development of the leaves, so that the most mature lesions are found on the upper parts of the outer leaves. Later lesions in all stages of development are found on the same plant. This type of development can be compared with that described by Smith (1929) for *Helminthosporium gramineum* causing leaf stripe of barley, where the developing leaves are each, in turn, in contact with the source of infection.

Secondary infection, on the other hand, is distinguished by the random distribution of the lesions, so that lesions at approximately the same stage of development can be found on all the leaves of a plant, or a single lesion may be found on an otherwise healthy plant. In commercial plantings, the source of the secondary infection can often be traced to a plant with primary infection. Secondary leaf infection can be very serious when it affects seedlings, because the leaves may be killed off before the corm is formed and the whole seedling then dies. A very good example of this was observed on one occasion when a grower complained of the death of some seedlings and suggested that it was the result of seed-borne infection. Examination of the situation showed that in fact the seedlings, planted in sterile soil and kept in a glasshouse until midsummer, had then been put outside near to some rows of cormlets of special cultivars. Several of these cormlets showed primary infection and the rows were close enough for spores to have been spread to the boxes of seedlings by rain splash. There is no evidence of seed-borne infection in this disease, nor any record of pycnidia occurring on the seed pods, though I have, on one occasion only, observed pycnidia on a flower bract. The plant concerned was a young one in a row of seedlings and was probably flowering for the first time.

Infection of young corms

Most of the young infected corms found at the end of a growing season will have been infected for the first time during that season. If this is the case, the leaves usually show a few secondary type lesions, with pycnidia, and the lower parts of the leaves, at or below the ground level, show brownish streaks. Small black sclerotial bodies similar in size to the pycnidia are present on the outer parts of the leaf bases, associated with the brown streaks. This basal infection is associated with a weft of mycelium spreading over the surface of the leaf bases, but no spores or pycnidia are normally found on these parts. Massey (1916) considered that the wash-down of spores through the soil was an important source of corm infection. The appearance of the continuous streaks and the presence of mycelium over large areas of the surface, suggests that at least some of the infection below the soil level is due to mycelium rather than spores. I have never observed germinating spores on the surfaces below soil level, though this in itself is no proof of their absence, since they might be easily rubbed off in digging up the plants for examination. However, the same symptoms occur when either large or small corms are planted below infected debris, consisting of sclerotia but no pycnidia or spores. In this case mycelium is the only source of infection; in the case of large corms, no pycnidia will be formed on the leaves, so that these cannot be a source of spores for infection of the basal parts. It therefore seems most likely that infection below soil level is due to mycelium growing out from infected areas at the soil surface, and spreading over the basal parts of the leaves, re-entering the host tissues at intervals.

The leaf bases sheathing the corm remain intact over the storage period, though they become dry and non-living. The sclerotia of *S. gladioli* persist on them and the fungus can be isolated from them quite easily throughout the storage period. The low relative humidity during storage does not kill the fungus, and experiments showed that it could survive for at least 10 weeks in a completely dry atmosphere. The position of the sclerotia on the brown areas of the leaf bases is not so easily seen during storage, since the whole of the leaf base (usually referred to as the husk) is dry and brown. When the husks are removed, small, irregular spots may be seen on the corm surface. They have a water-soaked edge, and are at first light brown in colour, becoming darker with age; the centre of the spot is sunken. In size they vary from spots about 2 mm. across to large sunken areas up to 20 mm. across, and usually irregular in outline. The infection does not penetrate deeply into the corm, usually only a few millimetres, and the infected part may often be prised away from the healthy tissue beneath, leaving a pit. Infection does not involve the vascular system. When the infection is well advanced, black sclerotia like those found on the husks may be seen on the surface of the lesions, and, on sectioning, are found within the infected tissue. Although the infection does not penetrate deeply into the corm, it may cause the death of young corms during storage, owing to the dry-out of the corm. However, most corms survive the storage period and are then the source of re-infection of the new season's corms during the following growing season.

Re-infection of corms

In considering the re-infection of corms, the method of reproduction of the gladiolus must be borne in mind. The gladiolus corm is a storage organ and its available nutrient material disappears as the new leaves are formed after planting. When the leaves are well developed, a new corm begins to form within the new leaf bases and above the corm of the previous year, and the new corm is fully developed at the end of the growing period. It was shown by Massey, and has never been disputed, that there is no direct infection of the new corm from the infected old corm through the stem tissues. This is what one would expect if the vascular system is never infected. It is therefore necessary to consider how the new corm becomes infected, as it nearly always does, when infected corms are planted. As each corm may produce two or more new corms plus a large number of cormlets, all of which are susceptible to infection, it is obvious that re-infection is a very important method of propagating the fungus and therefore of great importance to the grower of gladioli. The remarks which follow will apply equally to all ages of corm, infected in the previous season, and planted after storage. The only difference between young and old corms is that the young corms will show primary infection of the leaves, while older corms will not.

In order to observe the course of re-infection of the corms, a large number of infected corms was grown and corms were dug up at intervals throughout the growing season for examination. During the storage period, the corms are kept dry and little fungus growth seems to take place. When the corms are planted mycelium grows out from the sclerotia on the husks and from the lesions on the corm surface. The mycelium spreads over the corm surface and the husk and on to the young leaves which are beginning to grow out from the terminal bud. The first two leaves remain small and do not emerge above the soil but infection is visible on them in the form of dark streaks or spots and later by the appearance of sclerotia. As the new corm develops the first leaves die and are split away and rot, so that the first signs of infection are no longer visible at harvest.

The next signs of infection become clearly visible on the developing new corm about the beginning of July. At this stage, brown streaks appear on the inner leaf bases, and the first sclerotia are produced. Mycelium has spread over the surface for some time before the streaks are visible, but infection does not necessarily take place at all points of contact. Microscopical examination shows that the mycelium enters the host through stomata. On removing successive leaf bases, it is found that the mycelium and the resulting brown streaks have spread inwards, so that each leaf base in turn has become infected until the corm surface is reached. Corm lesions are most common at the base of the new corm and in many cases do not occur on the upper parts of the corm. The predominance of basal corm lesions had been noted by Massey (1916) and he was puzzled by it, because he considered that infection occurred through the washing-down of spores through the soil, which one would expect to produce infection on the upper parts of the corm. If, however, one considers that the source of infection lies below the new corm, or surrounds it in the form of infected husks, then the position of the lesions at the base is explicable. Furthermore, if the infection reaches the corm surface after growing through the surrounding husks, then the base of the new corm will be the part most quickly infected, because at the base there is only one leaf base covering the corm.

By the end of the growing season, the infected portions of the leaf bases have dried up somewhat, and sclerotia are present. The streaks may still be seen during the storage period by the experienced eye. Not only the main new corms, but also any cormlets produced from the old corm, may be infected. The cormlets are developed from lateral shoots in the axils of the leaves, and are therefore in a position to be infected in the same ways as the main corm surface. The cormlets have a very tough outer layer, on which the sclerotia may be found, and since thay can survive the winter in the soil they may be a serious source of infection in the soil for later crops. In *Gladiolus primulinus*, the cormlets are borne on long stolons which break through the leaf bases and extend up to 5 or 6 cm. from the mother corm. In this case, infection from one corm to the next in the row during the season might be possible.

When infected corms are harvested at the end of the season, they may often be distinguished by the fact that they are not so easily cleaned for storing as healthy corms. This is due to the fact that the lesions at the base prevent the new corm from separating readily from the old corm. If the corms are separated, the lesions may be pulled out from the base of the new corm, leaving pits. Since these lesions are in the region where the new roots will develop for the next season, they may have a serious retarding effect on growth at the beginning of the following year. The death of infected corms in the early part of the growing season can often be attributed to secondary infection of the corm by soil-inhabiting fungi, after failure of the impaired root system.

Infection of corms from inoculum in the soil takes place in the same way as this type of re-infection, and can be followed by planting corms under a layer of infected husks or other infected plant debris. The mycelium from the source of infection comes into contact with the outer leaf bases of the developing corms and infection follows. There is no evidence for free growth of the mycelium in the soil, so that infection only occurs when the source of infection is in direct contact with the susceptible corm.

There is thus a definite cycle of infection in this disease, related to the life history of the gladiolus. The fully grown gladiolus reproduces in three ways: seed, cormlets, and new large corms each season. Of these, only the seed is likely to be free from any infection. Cormlets from an infected corm may also be infected and on planting they will produce primary pycnidial infection on the leaves, which may spread to other plants, and further infected corms. The large corms produced from an infected large corm will also be infected, and on planting will give rise again to infected large corms plus infected cormlets and healthy seed. Chemical control of the disease has not so far proved entirely satisfactory, so that healthy stocks must be maintained if possible by growing only selected healthy corms. Rotation is also important, since infected debris in the soil will be a source of future infection.

The reaction of leaves to infection

It has been noted above that pycnidia are only formed on the leaves of seedlings and young plants of the large cultivars. The reason for this does not seem to have been considered by previous workers, and only a preliminary consideration of the problem is possible here. There are several hypotheses which might be put forward to explain the difference of reaction. One might suppose that the leaves of the older plants had a thicker cuticle and were thus able to resist penetration by the fungus. However, on investigation, this is not a feasible explanation since microscopical examination shows that the mycelium enters the leaf through the stomata. Furthermore, artificial inoculation of leaves of older plants, either with spores from young leaves, or with mycelium from pure cultures, results in infection. The resulting lesion is usually less clearly defined than a normal pycnidial lesion and no pycnidia are produced. Instead, sclerotia of the type found on the lower parts of the plant are produced, and no further development occurs even if the leaves are kept under moist conditions, such as those which would favour production of spores from pycnidia on young leaves.

Another possible explanation is that the growth rate of the larger plant is sufficiently fast for the leaf to escape infection, in cases of re-infection. However, when young and older corms are planted at the same level in the soil and their growth is measured, the result is the reverse. The leaves of young plants emerge from the soil from 5 to 6 days earlier than those of the older corms and their linear growth rate is as high or higher than that of those from the older corms. It therefore seems possible that there is some biochemical difference between young and old leaves, and perhaps between parts of the plant above and below ground level. Experiments *in vitro* have not revealed any medium capable of inducing abundant sporulation of this fungus, so that the nature of the difference cannot, as yet, be suggested.

The importance of the husk as a source of infection

Massey (1916) considered that the sources of corm infection were threefold: washing-down of spores through the soil on to the corms, infection of corms from fungus mycelium free in the soil, and infection from mycelium growing out from the old corm into the soil and then from the soil into the new corm. He found no evidence of direct growth of the fungus from the old corm to the new through the corm tissues. He noted, in his description of the disease, that 'in some cases the husk is also diseased' but continued: 'The lesion on the husk serves as an indication of the more important lesion underneath.' He does not describe the nature of the lesion on the husk.

The minute sclerotia on the husks were first noted by Drayton (1928), though he considered that they were incipient pycnidia. During my own examination of corms for experimental purposes, I found that these sclerotia were consistently present on the husks of diseased corms, and that the fungus could be isolated from the sclerotia on the dry husks. It was therefore clear that the sclerotia should be considered in any work on the sources of infection.

Preliminary experiments showed that healthy young corms could be infected by scattering dry infected husks over them at planting and it was therefore decided to set up further experiments to discover how far the incidence of the infection was affected by the presence of infected husks. The aim of the experiments was to discover how much infection was caused by fungus on the husks and how much by that on the corm itself. The first experiment (Expt. A in Table 1) was carried out in the first year, using fifty corms for each series and on a soil which was light and dry. A similar experiment (Expt. B in Table 1) was carried out in the following year, using one hundred corms for each series, on a heavier soil which tended to become waterlogged in wet weather.

In Exp. A, a total of 250 corms was used, giving fifty corms for each of five treatments. Each of these sets of fifty corms was divided into five groups of ten and the twenty-five groups thus obtained were planted in a Latin square. In Exp. B the same design was used but a total of 500 corms was available.

The treatments were as follows:

(1) Diseased corms, with sclerotia visible on the husks, planted without further treatment (IH).

(2) Diseased corms, with sclerotia visible on the husks, planted after removal of the husks as completely as possible (ID).

(3) Diseased corms, as in (2) above, planted with husks from definitely healthy corms replacing the diseased husks (ICH).

(4) Healthy corms planted after removal of husks and replacement by infected husks with visible sclerotia (CIH).

(5) Healthy corms with the husks intact were planted as a control (C).

Results of Exps. A and B are given in Table 1 as the proportion of infected new corms produced from either 50 (Exp. A) or 100 (Exp. B) old corms, and as the percentage of infected new corms. The disease incidence was recorded after removal of the husks from all corms, to ensure that no infection was accidentally overlooked. The results from the fiv groups of each variant were lumped together for the final scoring.

Table 1. *The effect of husks on re-infection by* Septoria gladioli

	Exp. A		Exp. B	
Treatment	Proportion corms infected	Percentage corms infected	Proportion corms infected	Percentage corms infected
IH	37/45	82·2	124/138	89·8
ID	26/66	39·4	115/121	95·0
ICH	37/66	57·8	118/155	76·1
CIH	66/69	95·7	154/161	95·7
C	1/71	1·4	0/182	0

The results show some interesting features. As one would expect, infected corms planted with the husks intact produced a high percentage of infected new corms. In Exp. A, removal of the husk (ID) was associated with a decrease in the percentage infection and an increase in the number of corms produced. In B, the reverse was the case; the percentage infection was greater than in series IH and the number of new corms produced was smaller. This suggests that some external factor may have affected the results, either in the effect of soil moisture on the spread of the mycelium (i.e. the dry conditions in Exp. A might have reduced the growth of the mycelium over the corm surface), or in some effect of the soil microflora, i.e. in Exp. B the reduced number of new corms might be partly accounted for by soil organisms having attacked the unprotected corms. Replacement of the infected husks by clean husks (ICH) resulted in slightly reduced infection in both Exps. A and B, and this was associated with an increase in the number of new corms as compared with series IH. This supports the suggestion made above that in Exp. B, removal of the husks (ID) had some unfavourable effect in that particular soil. The most conclusive and striking result is that of series CIH, where in both experiments infected husks placed over healthy corms produced a high percentage of infected new corms. It is thus shown that infected husks can be a very important source of inoculum for the disease. In the control plots only one corm was infected, and the source of this infection is not known.

It is therefore clear that the husks are an important source of infection in this disease, and, since husks may easily be left behind in the soil when the corms are harvested, they are a potential source of infection for any other crops of gladioli grown later in the same soil.

The persistence of the fungus in husks and corms

The aspect of the disease which has been most frequently considered has been control by various fungicidal treatments. Massey (1916) described various experiments on the control of the disease in the corm, none of which was successful. Since that time, many workers have tested fungicides, though none with complete success. One of the most complete recent accounts is that of Hawker (1944), who tested a large number of fungicides against this disease. Although some were effective against slight infections, she found that none of the treatments used killed the fungus completely within the corm and she assumed that the fungicidal effect shown was due to prevention of mycelial growth from the corm lesions. In all her experiments, the husks were removed before treatment. The treatment which she considered most effective was steeping the corms in 0·1 % mercuric chloride solution for 3 hr.

Following on the results of the experiments described above on the role of the husk in infection, it was decided to investigate the relative effects of fungicide on husks and corms. From the results obtained by Hawker and from my own preliminary experiments, it was decided that a solution of 0·1 % mercuric chloride + a wetter would be a suitable standard fungicide. Parallel experiments were set up to find the time required to kill the fungus in the husks and in the corms using the following techniques.

For investigation of the husks, infected portions with visible sclerotia were dipped in the solutions for periods varying from 1 min. to 3 days. After dipping, the husks were washed in sterile water to remove traces of mercuric chloride, and small portions were plated on to potato-dextrose agar. The remainder of the husks from each treatment was then scattered over healthy cormlets which were planted in pots in the glasshouse. The number of isolations from the platings was noted, and the appearance of leaf symptoms of disease on the young plants in the glasshouse acted as a second check on the survival of the fungus after treatment.

For investigation of the corms, infected corms, with the husks removed, were dipped in the solutions for times varying from 1 min. to 6 days. After dipping, the corms were washed in sterile water and small portions from the lesions were plated on to potato-dextrose agar. The corms were then planted in ground which had not previously grown gladioli, and at the end of the growing season the new corms were examined for the presence of disease. The results are shown in Table 2.

Table 2. *Persistence of* Septoria gladioli *after fungicidal treatment*

	Survival of *S. gladioli*			
Time of dip (0·1 % HgCl)	Corms plated	Corms in field	Husks plated	Husks in pots
1 min.	++	++	++	++
5 min.	++	++	++	++
15 min.	++	++	Contam.	++
1 hr.	++	++	Contam.	+
3 hr.	++	++	+	0
6 hr.	++	+	0	0
24 hr.	++	++	0	0
2 days	−	−	0	0
3 days	+	0	0	0
4½ days	++	0	−	−
6 days	0	+	−	−

++ = more than one isolation; + = one isolation only; 0 = no isolation; − = no test.

From Table 2 it can be seen that the time necessary to kill the fungus in the husk with 0·1 % mercuric chloride was 3–6 hr. None of the dipping times was sufficient to kill the fungus within the corm, and at the longer dipping times of 4½ and 6 days the corms themselves were severely damaged and several of the corms failed to grow. The persistence of the fungus in the corms is quite remarkable and clearly accounts for the failure of previous attempts to control the disease completely by the use of fungicides.

Discussion

The work reported here throws a new light on the life history of *S. gladioli* and suggests the lines along which control measures must be sought in the future. Three methods by which infection is spread are seen to be of importance in this disease:

(1) Old corm to new corm, or mother corm to cormlet infection.

(2) Infection of corms or cormlets from infected debris in the soil.

(3) Secondary spread by means of spores from plants showing primary leaf infections, in plantings of cormlets and seedlings.

Old corm to new corm infection is well recognized, although the mechanism of spread has not previously been made clear, and most recommended control methods are concerned with attempting to prevent it. The fact that mercuric chloride cannot kill the fungus in many of the lesions on the corms, but can kill the fungus on the corm scales suggests that fungicidal treatment of dehusked corms with a non-persistent fungicide is unlikely to eliminate the disease from a stock. Fungicidal treatment of intact corms, by killing the fungus in the corm scales, is likely to reduce the inoculum only to the level obtained by dehusking the corms. It therefore seems that more attention should be paid in future to the employment of fungicides which persist on the corm and thus continue to prevent growth of mycelium from the corm lesions.

Infection of corms and cormlets from infected debris in the soil is tacitly assumed in the literature, but the importance of the corm scales as a source of this infection has not been recognized. Although they have been shown experimentally to be an excellent source of inoculum, it is not yet clear whether detached scales or fragments are of great practical importance in contaminating a stock, particularly a stock of young corms or cormlets. Secondary spread from primary leaf infections is clearly of importance in plantings of young corms and cormlets. It is probably not difficult to control this spread by means of sprays, but growers do not at present pay enough attention to this and secondary infections of this type may well be the main cause of spread of the disease within the stock.

Until better control measures have been worked out, the best recommendations would seem to be the following. Only absolutely clean corms should be grown and these should be grown apart from all sources of infection, either from infected soil or from the proximity of infected stock. This last recommendation is particularly important when young corms and seedlings carrying the sporing stage of *S. gladioli* form a potential source of infection.

The work described here was carried out during the tenure of an Ethel Sargant Studentship at Girton College, Cambridge. My thanks are due to Dr N. F. Robertson for his encouragement and advice during the course of the work.

APPENDIX

List of infected specimens of European Gladiolus *species identified in the Kew and Cambridge Herbaria, showing the species and dates of collection.*

Species	Kew Herbarium	Cambridge Herbarium
G. byzantinus	Algiers, Apr. 1850 Algeria, Apr. 1851 ?, 1853	None
G. imbricatus	Czechoslovakia, 10 Aug. 1933 Czechoslovakia, 10 Aug. 1933 Transylvania, June 1862 Bulgaria, 2 August 1926 Poland, June 1894 Hungary, before 1897 Greece (Agrapha), 1885	Czechoslovakia, 1933 (same as Kew sheets)
G. illyricus	England (New Forest), 1879 France (Hyeres), 1867 Spain, 1860 Spain, 1925 Spain (Barcelona), Apr. 1847 Spain (Cartagena), 1852 Spain (Castile), before 1906 Caria, 1843 Cilicia, 19 May 1859 Portugal, 1879 Albania, 1900 Greece, 1885 Greece (Thrace), 1936	England (Brockenhurst, Hants), 4 July 1884 England (New Forest), July 1884 England (New Forest), July 1857 France (Vendee), 25 June 1853 Spain (Barcelona), 1874 Spain (Castile), no date
G. communis	Malta, no date France (Toulon), 1848	Sicily, May 1810
G. segetum	France (Puycasquier), no date no locality, 16 May 1863 Majorca, 6 May 1899 Persia, no date Persia, 1934 Madeira, Mar. 1837	Crete, Apr. 1846 Persia, no date (as Kew) Sicily (Avola), 20 Apr. 1856 Algiers, Apr. 1855 Syria, no date
G. dubius	France (Hyeres), 25 May 1871	None
G. palustris	Switzerland, before 1867 no locality or date	None
G. inarmensis	Italy, June 1874	None
G. neglectus	None	No locality, 1825

Note. The names of the *Gladiolus* species are those given on the herbarium sheets and no attempt has been made to check these identifications. Where a specimen is given a date 'before ...', this date has been derived from the dates of the collection to which it belongs. Specimens of the following species were examined, but none showed any examples of *Septoria gladioli*: *G. triphyllos*, *G. kotschyanus*, *G. aleppicus*, *G. persicus* and *G. halophilus*.

My thanks are due to the Director of the Royal Botanic Gardens, Kew, for permission to study the herbarium sheets of *Gladiolus* in the Kew Herbarium.

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SYMPODIELLA, A NEW HYPHOMYCETE GENUS

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(With Plate 30 and 2 Text-figures)

Sympodiella acicola gen.nov. sp.nov. a dematiaceous species inhabiting decaying needles of *Pinus sylvestris*, is described. The interesting development of its conidiophores and conidia is discussed. Cultural characteristics are briefly described, and ecological data are compared with those for a helicosporous form from the same habitat.

Sympodiella gen.nov.

Fungi Imperfecti hyphomycetes saprophytici.

Conidiophora solitaria, erecta vel ascendentia, simplicia, septata, atrobrunnea. *Conidia* acropleurogena, cylindrica, utrinque truncata, continua, hyalina, catenas siccas non ramosas formantes.

Typus generis:

Sympodiella acicola sp.nov. (Plate 30, Text-figs. 1, 2)

Mycelium atrobrunneum, sparsum, superficiale; *hyphae* atrobrunneae, septatae, prostratae, anastomosantes, reticulum in utraque pagina foliorum formantes. *Conidiophora* solitaria, atrobrunnea, apice pallide fusca excepta, simplicia, erecta vel ascendentia, septata, 26–280 μ longa, 2·2–3·6 μ crassa. *Conidia* acropleurogena, cylindrica, utrinque truncata, continua, hyalina, 7·4–14·0 μ longa, 1·6–2·4 μ crassa, catenas siccas non ramosas formantes. *Habitat* in foliis putridis *Pini sylvestris* L., Delamere, Cheshire, Anglia. *Holotypus* in Herb. I.M.I. No. 69967.

Sympodiella acicola forms a superficial network of darkly pigmented, septate, anastomosing hyphae (Pl. 30, fig. 2). The conidiophores are generally solitary, though occasionally several may be juxtaposed for part of their length (Pl. 30, fig. 1). They are simple, septate, and darkly pigmented except at the extreme apex, which is much lighter in colour, and 26–280 × 2·2–3·6 μ. The conidia are cylindrical when mature, slightly expanded then abruptly truncate at both ends, smooth, hyaline and continuous, 7·4–14·0 × 1·6–2·4 μ. They are borne acropleurogenously in dry, unbranched chains on the terminal portion of the conidiophore. A single conidiophore may produce more than twenty conidial chains, and one chain may consist of up to six conidia. The conidia are readily deciduous, though often remaining connected together in short chains after being shed.

If the mode of development of the conidiophores and conidia is examined, it is seen that *Sympodiella* may be placed in section II of Hughes's classification of the Hyphomycetes (Hughes, 1953). The first conidium is produced by a modification of the conidiophore apex. A new growing point develops just behind and to one side of this conidium, but almost immediately forms another conidium, to be replaced in turn by a further laterally developing growing point. As this process is repeated many times, the conidiophore increases in length in a sympodial manner, from which the generic name is derived. Acropetal, dry, unbranched chains of secondary conidia develop on the primary conidia by repeated extension and abstriction, growth being restricted to the terminal conidium of any chain. These processes are diagrammatically represented in Text-fig. 1. The diagrams are considerably simplified, as conidia are in fact borne on all sides of the conidiophore. A mature conidiophore from the natural substrate is shown in Text-fig. 2.

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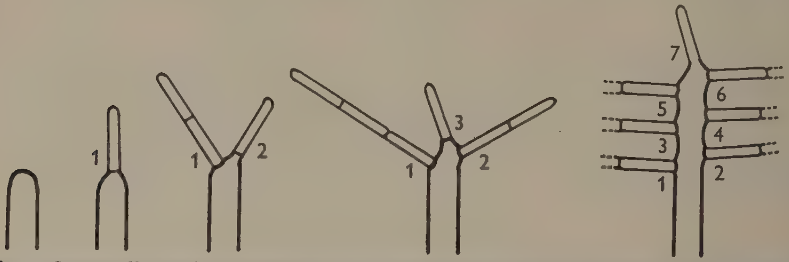
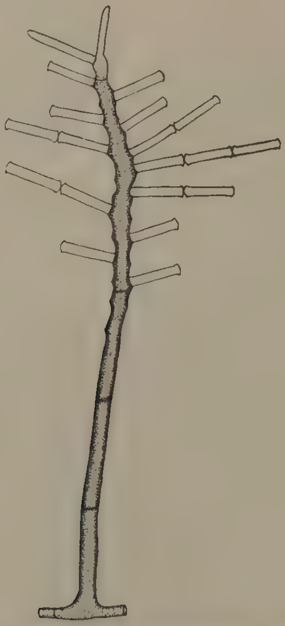


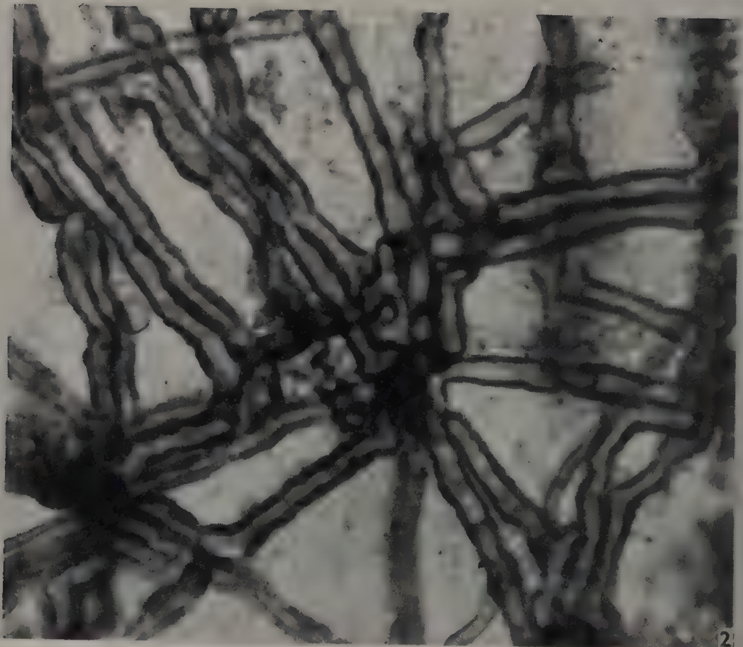
Text-fig. 1. *Sympodiella acicola.* Diagrammatic representation of the development of a conidiophore, and the formation of primary and secondary conidia. Primary conidia are numbered in the order in which they are produced.



Text-fig. 2. *Sympodiella acicola.* Mature conidiophore from the natural substrate. ×800.

The conidia germinate readily when picked off and plated on 2% malt extract agar, and the mycelium grows slowly, forming a restricted pulvinate

1



2

(*Facing p.* 521)

colony with an intensely black reverse, and a velvety brown-black aerial turf. Conidiophores develop in culture only after approximately two months. Some of the conidiophores observed in culture are once or twice branched, a phenomenon not seen on the natural substrate.

S. acicola was first observed in Sept. 1955, on decomposing needles of *Pinus sylvestris* from the F 1 layer of the Ao horizon of a podzol at Delamere Forest, Cheshire, England (Pl. 30, fig. 1). In Kendrick (1958*a*) *S. acicola* was referred to as 'Isolate 1/6', which was found on 89 % of needles of the F 1 layer examined, though absent from both L and F 2 layers immediately above and below the F 1. Thus *S. acicola* occurs in the same micro-habitat as *Helicoma monospora* Kendrick (1958*b*), and probably has similar nutritional requirements. Linder (1929) states that many of the saprophytic Helicosporae can successfully utilize either pectin or cellulose as their sole carbon source, and form a sparse, spreading mycelium on media containing these substances, though developing dense, pulvinate colonies on other substrates. As both *H. monospora* and *S. acicola* form sparse surface networks of creeping assimilative hyphae on the decaying pine needles, it seems probable that they attack the pectic substances of the middle lamellae, and the cellulose of the cell walls.

I would like to thank the following for their help and advice during the preparation of the manuscript; Prof. A. Burges, Dr D. Parkinson, and Dr V. H. Heywood, of the Botany Department, University of Liverpool; Dr M. B. Ellis and Mr E. W. Mason, of the Commonwealth Mycological Institute, Kew; and Dr S. J. Hughes, of the Canada Department of Agriculture, Botany and Plant Pathology Laboratories, Ottawa.

This study was carried out during the tenure of an Agricultural Research Council Research Studentship.

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EXPLANATION OF PLATE 30

Sympodiella acicola

Fig. 1. Naturally occurring conidiophores on a decaying needle of *Pinus sylvestris* from the F 1 layer of the Ao horizon. × 200.

Fig. 2. Reticulum of anastomosing assimilative hyphae on the needle surface. × 1500.

(*Accepted for publication* 10 *February* 1958)

REVIEWS

The U.C. System for producing Healthy Container-grown Plants. Ed. K. F. Baker. (Manual Ext. Serv. Cal. agric. Exp. Sta. 23, 1957). Pp. 332, 136 figures. Price: $1.00.

The University of California system for producing healthy container-grown plants has been developed around the use of standard soil mixes for glasshouse and nursery crops. The U.C. soil mixes are a further development of the principle underlying the original John Innes composts, which has now been carried to its logical conclusion. The two prime ingredients are fine sand and acid peat moss (sphagnum or hypnum types), and these form the physical framework of the 'soil' but are chemically inert, so that all nutrients except trace elements must be added to the mix as fertilizers. Five standard mixes, varying in proportion of fine sand to acid peat moss, are recommended for a wide range of growing requirements. Amongst various advantages claimed for the U.C. soil mixes are: (1) strict control of nutrients, all of which have to be added as fertilizers to the original mix; (2) equally strict control of physical properties, according to the type of mix selected for any particular purpose; (3) complete avoidance of the phytotoxicity that often develops after heat treatment of soils and composts, and especially of soils with a high organic content; (4) greater efficiency in disease control.

The practical research by the University of California that has produced these soil mixes has been extended into every sphere of plant culture in glasshouses and nurseries. Fertilizer regimes, partial sterilization of the soil by heat and by fumigants for control of weeds, pests and diseases, production of healthy planting stock and mechanization of plant production have all received equally thorough investigation. Although this admirable hand-book has been designed primarily for Californian growers, no plant pathologist ought to be deceived by a parade of some familiar facts, often necessarily repeated, into thinking that he has nothing fresh to learn here. All pathologists could profit from the discussion by K. F. Baker in Section 3 on how best to reconcile the conflicting requirements for control of a number of diseases occurring together in actual practice, with the complication of a salinity problem thrown in for good measure.

This book is an object lesson in the practical achievements that can be accomplished by a determined team of research workers for an agricultural industry. In addition to *ad hoc* research, excellent use has been made of a wide range of published research in soil science. Thus Section 6, by O. A. Matkin, P. A. Chandler and K. F. Baker, contains a useful summary of knowledge about the causes of soil toxicity resulting from partial sterilization, due to temporary excess of ammonium nitrogen, etc. Section 14 on 'Beneficial soil micro-organisms' by John Ferguson can be strongly recommended for general reading, especially for its discussion of possible developments in controlled microbial recolonization of partially sterilized soils. So can Section 15 on 'Importance of variation and quantity of pathogens' by R. D. Durbin.

Prof. K. F. Baker, who has acted as editor, and who is also author or co-author of nine out of the seventeen sections, is greatly to be congratulated on this corporate achievement. There is a wide bibliography, an exhaustive index, and a glossary for the non-professional reader. For English users, the second edition might well include a brief glossary of English equivalents to American usages of some common words. Thus throughout this book, the word 'presently' is obviously intended to mean 'at the present time', a usage that the *Oxford Dictionary* gives as obsolete; users of this term over here now understand it to mean 'before long' or 'soon', so that the U.S.A. has now become the repository of the original truth. At a price of $1.00, this manual is certainly an exception to the general impression that American books are expensive by comparison with their English counterparts; the production is excellent except for the binding, which will not stand up to the handling it will certainly get.

S. D. GARRETT

Handbuch für Pilzfreunde. Erster Band. *Die wichtigsten und häufigsten Pilze* (*mit besondere Berücksichtigung der Giftpilze*). By Edmund Michael, edited and revised by Bruno Hennig. (Jena: Gustav Fischer Verlag. 1958.) Pp. viii + 260, 202 col. figures, 17 text-figures. Price: DM. 36.50.

This ambitious work represents the culmination of a project initiated in 1895 with the issue of a single volume with 47 illustrations. By 1902 it had extended to two volumes 175 illustrations) and three by 1905 (206 illustrations). A fourth is now in view, the others being enlarged and revised: vol. II, *Nichtblätterpilze*, with coloured illustrations of 300 species, is promised for next spring; vol. III, *Blätterpilze* (*Hellblättler mit Einschluss der Milchlinge und Täublinge*), 250 species, probably in 1960; and vol. IV, *Blätterpilze* (*Dunkelblättler—Schwarz- und Braunsporer*), 250 species, in 1961.

In the present volume there are 22 introductory chapters (128 pp.), designed to offer the would-be fungus-hunter all the necessary basic information for an identification. Interesting features of this section are a 2-page colour chart of 50 colours (with a key in Latin and German), a chapter on odours, grouped and subdivided, with specific examples of each (8 pp.), and a comprehensive 5-page bibliography. As there are no keys to the genera and species, identification must be, in the first instance, from the coloured plates, being checked from the accompanying description, which is usually adequate for the macroscopic characters of these well-known species.

Eleven artists are concerned in the production of the originals for the coloured plates and there is thus some variation in standard; some are excellent, others have been allowed some artistic licence, particularly in regard to the substratum (often depicted as an unidentifiable moss or grass), which detracts from their scientific value. Spores are not drawn and cystidia are not mentioned.

The mycologist, as distinct from the mycophagist and the mere collector, may be a little disturbed to have the species of one genus segregated into two or more volumes, while the tendency of the nomenclature to run with the hare and hunt with the hounds in such citations as *Rhodophyllus* (*Entoloma*) *clypeatus* and *Oudemansiella* (*Mucidula, Collybia*) *radicata* may be confusing.

The book is well produced, the paper is glossy throughout, and it should be useful to a beginner who is more familiar with German than with English. G. M. WATERHOUSE

An Introduction to Medical Mycology. By G. M. Lewis, Mary E. Hopper, J. W. Wilson and O. A. Plunkett. 4th edition. (Chicago: Year Book Publishers Inc. 1958.) Pp. 453, 2 coloured plates, 135 text-figures. Price $15.00 (£5. 15s.)

This is virtually a new book. The authors have increased from two to four, the number of pages from 336 to 453 and the text-figures from 103 to 135 while, in conformity with prevailing trends, the price has more than doubled. The separation of clinical and mycological aspects characteristic of the earlier editions has been replaced by a series of integrated accounts of the mycoses treated but, as before, there is emphasis on the superficial mycoses (pp. 1–245)—and on ringworm in particular. The nomenclature of the pathogens has been renovated, the bibliographies have been modernized and the index has been improved. The excellence of the clinical photographs has been maintained but the numerous new black and white text-figures (of which many are also reproduced in Funder's *Practical Mycology*, 1953) are in general less satisfactory. Of the new authors, Dr Wilson has re-written the chapters on the deeper mycoses (pp. 246–365) and Dr Plunkett has contributed a chapter (pp. 423–40) on some of the commoner fungal contaminants. A continued popularity for 'Lewis and Hopper' appears to be assured.

G. C. AINSWORTH

Clasterosporium *and some Allied Dematiaceae-Phragmosporae.* I. By M. B. Ellis. (Kew, Surrey: Commonwealth Mycological Institute [Mycological Papers, No. 70], 1958.) 89 pp., 63 text-figures. Price: 30*s.*

This paper gives keys to, and full descriptions of, 7 species of *Clasterosporium*, 2 of *Ceratophorum*, 50 of *Sporodesmium*, and 4 of *Annellophora.*

INDEX†

New names are indicated by an asterisk

Acrostalagmus cinnabarinus, 76
Actinospora megalospora, 110, 111
Adlakha, K. L., *see* Reid, D. A.
Agaricus molluscus, 433
Agropyron repens, fungi on decaying, 165–177
Air spora, 145–156, 449
Alatospora acuminata, 110
Alternaria tenuis, 153, 169–172
*Anguillospora crassa, 367
  longissima, 110
Apple scab, 392–393
Aquatic fungi, 365
Armillaria mellea, 157–164
Arthrobotrys dactyloides, 341–364
Aspergillus nidulans, 40, 48, 501
  niger, 40, 48
  versicolor, 501
Asteromyces cruciatus, 64
Atkins, G. A., Hindson, W. R. and Russell, A. B. '*Emericella nidulans* (Eidam) Vuill. var. *aurantiobrunnea* var. nov and its *Aspergillus* state', 501–504

Balfour-Browne, F. L., *see* Reviews
Barley leaf blotch, 99–108
Barton, R. 'Occurrence and establishment of *Pythium* in soils', 207–222
Basidiospores of the air spora, 150–151
Batko, S., Murray, J. S. and Peace, T. R. '*Sclerophoma pithyophila* associated with needle-cast of pines and its connexion with *Pullularia pullulans*', 126–128
Batts, C. C. V. and Jeater, Ann. 'The development of loose smut (*Ustilago tritici*) in susceptible varieties of wheat, and some observations on field infection', 115–125
Belonopsis graminea, 386
Booth, C. 'Studies of pyrenomycetes. III. *Otthia spiraeae* (Fuckel) Fuckel, syn. *Diplodia sarmentorum* (Fr.) Fr.', 335–340
British Mycological Society (1957):
  Annual General Meeting, 264
  Forays, Dublin (autumn), 387; Porlock (spring), 266
  Proceedings, 263–264, 392–396
British Records, *17–20*, 64; *21–24*, 261; *25–28*, 385
Brown, Juliet C. 'Fungal mycelium in dune soils estimated by a modified impression slide technique', 81–88
  and Kendrick, W. B. '*Gliomastix gulluliformis* sp.nov.', 499–500
Butler, Gillian M. '*Uromyces* in a population of *Euphorbia cyparissias*', 401–404
Buxton, E. W. 'Pathogenic variation in *Fusarium oxysporum*' (abs.), 396

Cammack, R. H. 'Studies on *Puccinia polysora* Underw. I. The world distribution of forms of *P. polysora*', 89–94
Campylospora chaetocladia, 110, 112–113
Candida albicans, 322
  curvata, 322
  guilliermondii and var. membranifaciens, 322
  mycoderma, 322
  parapsilosis, 322
  pelliculosa, 322
  tropicalis, 322
Carex paniculata leaf litter fungi, 185–195
Carrot licorice rot, 223–226
Cash, Edith K. and Corner, E. J. H. 'Malayan and Sumatran discomycetes', 273–282
Catinella olivacea, 277
Cellophane disk technique, 14–16
Centrospora acerina, 223–226
Cephalosporium, 76, 450
  acremonium, 185
Cercosporella herpotrichoides, spore dispersal of, 449–456
Chaetostylum, 135, 139
Chytrid on *Mucor*, 315
Chytridium suburceolatum, 318
Chytriomyces hyalinus, 261–262
Cladosporium, 152
  herbarum, 169–172, 185
*Clavaria indica, 205
  *lithocras, 438
Clavariopsis aquatica, 110
*Clavulina mussooriensis, 204
Conidiobolus rhysosporus, 52–54
Cookeina sulcipes, 273
Coprinus flocculosus, 429
  insignis, 430
  rostrupianus, 429
  *saichiae, 429
  sylvaticus, 429
  tardus, 429
Corner, E. J. H., Thind, K. S. and Dev, S. 'The Clavariaceae of the Mussoorie Hills (India). IX', 203–206
  see Cash, Edith K.
*Craterellus cymatodermoides, 131
  *mussooriensis, 132
Crosse, J. E., *see* Reviews
Cunnell, G. J. 'On *Robillarda phragmitis* sp.nov.', 405–412
Cylindrocarpon, 74, 76, 78
Cyphella fraxinicola, 439
  lactea, 438
  ochroleuca, 438
  rubi, 438

Dactylella doedycoides, 341–364
Daedalia biennis, 434

---

† See also pp. 187–190 (lists of fungi from *Carex* leaf litter).

Damping-off, factors affecting, 483–490
Dasyscypha brasiliensis, 277
  *bruneo-maculata, 277
  cingregata, 277
  inspersa, 277
  plebia, 278
Day, P. R. 'Mutation to virulence in plant pathogens' (abs.), 395
Deighton, F. C., *see* Reviews
Dev, S., *see* Corner, E. J. H.
Dimorphospora foliicola, 412
Diplodia sarmentorum, 335–340
Discomycetes of Malaya and Sumatra, 273–282
Dring, Vivienne J. '*Conidiobolus rhysosporus* Drechsler in Great Britain', 52–54
Durella suecica, 385

Eccilia molluscus, 433
*Emericella nidulans var. aurantiobrunnea, 501–504
*Encoelia singaporensis, 278
England, D. J. F., *see* Morton, A. G.
Epicoccum purpurascens, 169–172
Erysiphe, 153
  cichoracearum, 17, 29, 34–35
  graminis, 17, 24–30, 34–37
  umbelliferarum, 17, 29, 35
Eucalyptus marginata, yellow straw rot of, 95–98
Euphorbia cyparissias, Uromyces on, 401–404

Farley, Jacqueline O. 'The isolation and identification of yeasts contaminating cattle tongue epithelial cultures of the virus of foot-and-mouth disease', 320–324
Fayodia bisphaerigera, 423
Flagellospora curvula, 110
Fowler, Daphne A., *see* Morton, A. G.
Francis, S. M., *see* Reviews
*Fulminispora, 369, 412
  *ovalis, 369, 412
Fusarium, 74, 76, 78
  culmorum, 185, 449, 453
  oxysporum, 396

Galactinia retiderma, 273
Garrett, S. D. 'Inoculum potential as a factor limiting lethal action by *Trichoderma viride* Fr. on *Armillaria mellea* (Fr.) Quél.', 157–164
Gladiolus, Septoria on, 505–518
Glaux maritima rust, 178–184
Gliocladium, 74
  roseum, 76, 78
*Gliomastix guttuliformis, 499–500
Gloeotinia temulenta, 461–482
Gregory, P. H. 'A correction', 202
  and Sreeramulu, T. 'Air spora of an estuary', 145–156
  and Stedman, O. J. 'Spore dispersal in *Ophiobolus graminis* and other fungi of cereal foot rots', 449–456
  see Reviews
Griffin, D. M. 'Influence of pH on the incidence of damping-off', 483–490
Griffiths, D. J. 'Physiological specialization of oat crown rust (*Puccinia coronata* Corda f. sp. *avenae* (Erikss. & Henn.) Erikss.', 373–384
Griffiths, E. 'Sexual reproduction and variation in *Gloeotinia temulentum* (Prill. & Delacr.) Wilson & Gray', 461–482

Harvey, R. 'Sporophore development and proliferation in *Hydnum auriscalpium* Fr.', 325–334
Haglundia perelegans, 261
Helicobasidium purpureum, 283–308
*Helicoma monospora, 446–448
Helicostylum, 135–141
  elegans, 135–140
  *fresenii, 139
  pyriforme, 135–137
  *venustellum, 140
Helminthosporium hyalospermum, 172–173
Helotium crocatum, 278
  geogenum, 64
  *hinnuleum, 278
  laetum, 64
  velhaense, 279
Heterosporus biennis, 343
Hickman, C. J. 'Presidential address. *Phytophthora*—plant destroyer', 1–13
Hindson, W. R., *see* Atkins, G. A.
Hirst, J. M. 'Quantitative studies of apple scab (abs.)', 393
Hudson, H. J. and Webster, J. 'Succession of fungi on decaying stems of *Agropyron repens*', 165–177
Hydnum auriscalpium, 325–334
*Hymenochaete fusco-badia, 133

Ingold, C. T. 'Aquatic fungi from Uganda and Rhodesia', 109–114
  'New aquatic hyphomycetes: *Lemonniera brachycladia, Anguillospora crassa* and *Fluminispora ovalis*', 365–372
  'Physiological study of spore discharge in *Sordaria*' (abs.), 394

Jeater, Ann, *see* Batts, C. C. V.
Jinks, J. L. 'Cytoplasmic variation in fungi (abs.)', 394

Karlingia asterocysta, 262
  rosea, 309–315
Kendrick, W. B. '*Sympodiella*, a new hyphomycete genus', 519–521
  '*Helicoma monospora* sp.nov. from pine litter', 446–448
  see Brown, Juliet C.
Kerr, A. 'The use of cellophane in growth studies on soil fungi', 14–16
Kulkarni, U. K. 'Studies in the development and cytology of *Puccinia penniseti* Zimm.', 65–73

La Touche, C. J., *see* Reviews
*Lemonniera brachycladia, 365
Lentinellus cochleatus, 442
Lentinus adhaerens, 422
  cochleatus, 422
  pulverulentus, 422
  resinaceus, 422
Lepiota eriphora, 426
  metulaespora, 427
  *ventriospora, 427

Leptosphaeria microscopica, 169–172
  nigrans, 172
Leveillula taurica, 17–38
Lunulospora curvula, 110
Lyophyllum favrei, 419
Lythgoe, J. N. 'Taxonomic notes on the genera *Helicostylum* and *Chaetopstylum* (Mucoraceae)', 135–141

Macdonald, J. A. 'Two biological races of *Uromyces lineolatus* (Desm.) Schroet.', 178–184
Maize rust, 89–94
Malcolmson, Jean F. 'A consideration of the species of *Phoma* which parasitize potatoes', 413–418
Manners, J. G., *see* Reviews
Medicago, Uromyces on, 402–404
Metasphaeria cumana, 185
Mollisia isabellina, 279
  palustris, 172–173
Mortierella, 74, 76, 78
Morton, A. G., England, D. J. F. and Towler, Daphne A. 'The physiology of sporulation in *Penicillium griseofulvum* Dierckx', 39–51
Mucor, 185, 315
Muller, H. G. 'The constricting ring mechanism of two predacious hyphomycetes', 341–364
Murray, J. S., *see* Batko, S.
Mycelium in dune soils, 81–88
Mycena bisphaerigena, 423
  megaspora, 424
  uracea, 424
Mycoleptodon microcystidius, 437
Mycosphaerella recucita, 173

Nasturtium, *see* Watercress
Nidularia sect. Sorosia, 55–63
  arundinacea, 60, 62
  castanea, 55
  denudata, 55–59, 62
  duriaena, 55, 57, 59
  farcta, 62
  minutissima, 55, 59–62, 57
Nour, M. A. 'Studies on *Leveillula taurica* (Lév.) Arn. and other powdery mildews', 17–38

Oenanthe croccata rust, 178–184
Ombrophila microspora, 280
Omphalia bisphaerigera, 423
*Omphalina obscurata, 419
Oespora pustulans, 392
Ophiobolus graminis, spore dispersal of, 449–456
  herpotrichus, 172
*Orbilia fici, 280
  leucostigma, 280
Otthia spiraeae, 335–340; synonymy of, 335
Owen, H. 'Physiological specialization in *Rhynchosporium secalis*', 99–108

Palmer, J. T. 'Observations on Gasteromycetes. VI. Three British species of *Nidularia* Fr. Section Sorosia Tul.: Ecology and distribution', 55–63
Paterson, R. A. 'On the planktonic chytrids *Zygorhizidium melosirae* Canter and *Z. planktonicum* Canter', 457–460
Pellicularia praticola, 14–16
Penicillium, 185
  frequentans, 40, 48
  griseofulvum, 39–51
  melinii, 40, 48
  thomii, 40, 48
Pennisetum typhoides, Puccinia penniseti on, 65, 66, 68–72
Pezicula myrtillina, 385
Pezizella hamulata, 64
Phaedropezia epispartia, 273
Phaeocyphella fraxinicola, 439
  ochroleuca, 438
Phellinus ferreus, 434
Phillipsia carneicolor, 273
Phoma eupyrena, 413–418
  foveata, 413–418
  solanicola, 413–418
  tuberosa, 413–418
Phragmites communis, Robillarda on, 405–412
Phytophthora, review of, 1–13
  drechsleri, 200
  gonapodyides, 196–198
  megasperma, 199
  *oryzae, 200
  syringae, 201
Pichia farinosa, 322
Pine needle-cast, 126–128
Pisum sativum root fungi, 74–80
Pleospora trichostoma, 174
  vagans, 169
Pluteus minutissimus, 425
  psichriophorus var. minutissimus, 425
Poria ambigua, 436
  consobrinoides, 436
  ferrea, 267
  *healeyi, 95–98
  lacerta, 436
  reticulato-marginata, 436
Potatoes, Phoma on, 413–418
Puccinia coronata f. sp. avenae, 373–384
  penniseti, 65–73
  polysora, 89–94
Pugh, G. F. J. 'Leaf litter fungi found on *Carex paniculata* L.', 185–195
Pullularia pullulans, 323
Pulvinula etiolata, 274
  globifera, 274
Pyronema omphalodes, 274
Pythiomorpha fischeri, 201
  gonapodyides, 196
  miyabeana, 199
  oryzae, 200
  undulata, 199
Pythium, 74, 76, 78
  debaryanum, 212
  mamillatum, 207–222
  ultimum, 212, 483–490
  undulatum, 199

*Ramaria brevispora, 203
  *brevispora var. albida, 204
Ramularia, 169

Reid, D. A. 'New or interesting records of British hymenomycetes. II.', 419–445
  , Thind, K. S. and Adlakha, K. L. 'The Thelephoraceae of the Mussoorie Hills (India)', 129–135
  see Reviews
Reviews:
  Baker, K. F. (ed.), The U.C. system for producing healthy container-grown plants, 1957 (by S. D. Garrett), 522
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  and Malencon, Uredinées du Maroc, 1957 (by J. G. Manners), 399
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  Smith, A. H., Mushroom hunter's field guide, 1958 (by Sheila M. Francis), 399
  Vanbreuseghem, R., Mycoses of man and animals, 1958 (by C. J. La Touche), 398
Rhodophyllus molliusculus, 433
Rhodotorula mucilaginosa, 322
Rhynchosporium secalis, 99–108
Robillarda, 411
  *phragmitis, 405–412
Russell, A. B., *see* Atkins, G. A.

Salt, G. A. '*Oospora pustulans* as a parasite of potato roots (abs.)', 392
*Sarcosoma umbrinum, 274
Scirpus maritimus rust, 178–184
Scleroderris callunigena, 261
  *sumatrana, 280
Sclerophoma pithyophila, 126–128
Scutellina stenosperma, 385
Sebacina laccata, 267
Selenophoma donacis, 173, 175
Septoria gladioli, 505–518
Shepherd, Audrey M., *see* Reviews
Solanum melongena, Puccinia penniseti on, 65, 68
Sordaria fimicola, 394
Sparassis crispa, 441
  laminosa, 441
  *simplex, 439
*Spathularia heterospora, 281
*Sphaerosoma malayense, 275
Sphaerotheca fuliginea, 17, 29, 34–35
*Spongospora subterranea f. sp. nasturtii, 491–498
Sporobolomyces, 147–150
  roseus, 322
Sreeramulu, T., *see* Gregory, P. H.
Srivastava, S. N. S. 'Some studies on *Centrospora acerina* (Hartig) Newhall, the cause of licorice rot of carrot', 223–226
Stamps, D. Jean, *see* Reviews
Stedman, O. J., *see* Gregory, P. H.
Stemphylium, 153
Stenton, H. 'Colonization of roots of *Pisum sativum* L. by fungi', 74–80
Stereum abietinum, 441
  ochraceo-flavum, 444
  *sparassoides, 129–131
  sulphuratum, 442
Stone, Owen M. 'Some observations on *Septoria gladioli* Pass.', 505–508
Storey, I. F. 'The source and control of apple scab infection at Wisbech' (abs.), 392
Stysanus stemonites, 185
*Sympodiella, 519–521
  *acicola, 519–521

Talboys, P. W. 'Some mechanisms contributing to *Verticillium*-resistance in the hop root', 227–241
  'Degradation of cellulose by *Verticillium albo-atrum*', 242–248
  'Association of tyloses and hyperplasia of the xylem with vascular invasion of the hop by *Verticillium albo-atrum*', 249–260
Tetrachaetum elegans, 110
Tetracladium marchalianum, 110
  setigerum, 110
Tetraploa aristata, 172
Thelephora sparassoides, 129
Thamnidium chaetocladoides, 136
Thind, K. S., *see* Corner, E. J. H., Reid, D. A.
Thyridaria minima, 267
Tilletiopsis, 150
Tomlinson, J. A. 'Crook root of watercress. III. The causal organism *Spongospora subterranea* (Wallr.) Lagerh. f. sp. *nasturtii* f. sp. nov.', 491–498
*Trametes serpens subsp. albida, 437
?Tricelophorus sp., 371
  monosporus, 110

Trichoderma viride, 157–164, 185, 207, 213
Tricholoma favrei, 419
Trichosporon capitatum, 322
  cutaneum, 322
Tricladium angulata, 110
Trifolium, Uromyces on, 402–404

Unguiculella falcipila, 64
  hamatula, 64
Uromyces lineolatus and f. spp. glaucis-scirpi and scirpi-oenanthecrocata, 178–184
  pisi, 402, 404
  scutellatus, 401–404
  striatus, 401–404
Ustilago, 153
  tritici, 115–125

Valder, P. G. 'The biology of *Helicobasidium purpureum* Pat.', 283–308
Verticillium albo-atrum, 227–260

Walters, N. E. M. '*Poria healeyi* sp.nov. the causal fungus of yellow straw rot in Jarrah (*Eucalyptus marginata* Sm.)', 95–98
Warcup, J. H., *see* Reviews
Watercress crook root, 491–498
Waterhouse, Grace M. 'The invalidity of the genus *Pythiomorpha*. II.', 196–202

Webster, J., *see* Hudson, H. J.
Wheat loose smut, 115–125
Willoughby, L. G. 'Studies on soil chytrids. III. On *Karlingia rosea* Johanson and a multi-operculate chytrid parasitic on *Mucor*', 309–319

Zygorhizidium melosirae, 457–460
  planktonicum, 457–460

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CONTENTS

PAGE

Uromyces in a population of *Euphorbia cyparissias.* By Gillian M. Butler 401

On *Robillarda phragmitis* sp.nov. By G. J. Cunnell (With 3 Text-figures) 405

A consideration of the species of *Phoma* which parasitize potatoes. By Jean F. Malcolmson. (With Plate 22) 413

New or interesting records of British hymenomycetes. II. By D. A. Reid. (With Plates 23 and 24 and 28 Text-figures) 419

Helicoma monospora sp.nov. from pine litter. By W. B. Kendrick. (With Plate 25) . 446

Spore dispersal in *Ophiobolus graminis* and other fungi of cereal foot rots. By P. H. Gregory and O. J. Stedman. (With 3 Text-figures) 449

On the planktonic chytrids *Zygorhizidium melosirae* Canter and *Z. planktonicum* Canter. By R. A. Paterson. (With 1 Text-figure) 457

Sexual reproduction and variation in *Gloeotinia temulenta* (Prill. & Delacr.) Wilson & Gray. By E. Griffiths. (With Plate 26 and 1 Text-figure) 461

Influence of pH on the incidence of damping-off. By D. M. Griffin. (With 1 Text-figure) 483

Crook root of watercress. III. The causal organism *Spongospora subterranea* (Wallr.) Lagerh. f.sp. *nasturtii* f.sp.nov. By J. A. Tomlinson. (With Plate 27 and 4 Text-figures) 491

Gliomastix guttuliformis sp.nov. By Juliet C. Brown and W. B. Kendrick. (With Plate 28 and 1 Text-figure) 499

Emericella nidulans (Eidam) Vuill. var. *aurantiobrunnea* var.nov. and its *Aspergillus* state. By G. A. Atkins, W. R. Hindson and A. B. Russell. (With Plate 29) . 501

Some observations on *Septoria gladioli* Pass. By Olwen M. Stone. (With 1 Text-figure) 505

Sympodiella, a new hyphomycete genus. By W. B. Kendrick. (With Plate 30 and 2 Text-figures) 519

Reviews 522

Index 524

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